Ecological Modelling 371 (2018) 76–89

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

# Exploring adaptation strategies of coffee production to climate change using a process-based model

Eric Rahn[a,b,c,*], Philippe Vaast[d,e], Peter Läderach[b], Piet van Asten[c,f], Laurence Jassogne[c], Jaboury Ghazoul[a]

[a] Swiss Federal Institute of Technology (ETH) Zurich, Environmental Systems Science, Switzerland
[b] International Center for Tropical Agriculture (CIAT), Cali, Colombia
[c] International Institute of Tropical Agriculture (IITA), Kampala, Uganda
[d] World Agroforestry Centre (ICRAF), Hanoi, Viet Nam
[e] Centre de Coopération International en Recherche Agronomique pour le Développement (CIRAD), Eco&Sols, Université de Montpellier, France
[f] Olam International Ltd., Kampala, Uganda

ARTICLE INFO

*Keywords:*
*Coffea arabica* L.
Agroforestry system
Spatial decision support
Adaptation to climate change
Parameter uncertainty

ABSTRACT

The response of coffee (*Coffea arabica* L.) agronomical performance to changes in climate and atmospheric carbon dioxide concentration ([$CO_2$]) is uncertain. Improving our understanding of potential responses of the coffee plant to these changes while taking into consideration agricultural management is required for identifying best-bet adaptation strategies. A mechanistic crop modelling approach enables the inclusion of a wide range of prior knowledge and an evaluation of assumptions. We adapt a model by connecting it to spatially variable soil and climate data, by which we are able to calculate yield of rain-fed coffee on a daily time-step. The model takes account of variation in microclimate and water use as influenced by shade trees. The approach is exemplified at two East African sites with distinctly different climates (Mt. Elgon, Uganda, and Mt. Kilimanjaro, Tanzania) using a global sensitivity analysis for evaluation of model behavior and prior parameter uncertainty assessment. We use the climate scenario driven by the Hadley Global Environment Model 2-Earth System representative for the year 2050 to discuss potential responses of the coffee plant to interactions of elevated [$CO_2$], temperature, and water availability. We subsequently explore the potential for adaptation to this scenario through shade management. The results indicate that under current climatic conditions optimal shade cover at low elevations (1000 m.a.s.l.) is 50%, provided soil water storage capacity is sufficient, enabling a 13.5% increase in coffee yield compared to unshaded systems. Coffee plants are expected to be severely impacted (ranging from 18% to 32% coffee yield reductions) at low elevations by increased temperature (+2.5 °C) and drought stress when no elevated [$CO_2$] is assumed. Water competition between coffee and shade trees are projected to be a severe limitation in the future, requiring careful selection of appropriate shade tree species or the adoption of other technologies like conservation measures or irrigation. The [$CO_2$]-fertilization effect could potentially mitigate the negative effect of temperature increase and drought stress up to 13–21% depending on site conditions and will increase yield at higher altitudes. High uncertainty remains regarding impacts of climate change on flowering. The presented model allows for estimating the optimal shade level along environmental gradients now and in the future. Overall, it shows that shade proves to be an important adaptation strategy, but this requires improved understanding regarding site-specific management and selection of tree species. Moreover, we do not yet include climate change uncertainty.

## 1. Introduction

Coffee is cultivated in over 70 countries throughout the tropics with approximately 60% of the production being *Coffea arabica* L. (Arabica coffee) and 40% being *Coffea canephora* Pierre ex Froehner, syn. *Coffea robusta* (Robusta coffee) (FAO, 2015). Over 70% of the world's coffee is produced by smallholders managing less than 10 ha of land (Fridell, 2014). Climate change is expected to have substantial impacts on suitable areas for coffee (*C. arabica*) cultivation (Bunn et al., 2015a; Ovalle-Rivera et al., 2015; Magrach and Ghazoul, 2015), pests and diseases pressure (Jaramillo et al., 2011; Magrach and Ghazoul, 2015) and genetic resources (Davis et al., 2012), thereby likely changing the

* Corresponding author at: ETH Zurich, CHN H 71, Universitätsstrasse 16, 8092 Zürich, Switzerland.
*E-mail address:* eric.rahn@usys.ethz.ch (E. Rahn).

https://doi.org/10.1016/j.ecolmodel.2018.01.009
Received 31 July 2017; Received in revised form 19 January 2018; Accepted 22 January 2018
0304-3800/ © 2018 Elsevier B.V. All rights reserved.

agro-ecological zones most suitable for coffee production (Bunn et al., 2015b). Agroforestry systems can both contribute to climate change mitigation while potentially enabling adaptation to climatic changes (Matocha et al., 2012; Mbow et al., 2014; Vaast et al., 2016).

Due to the perennial nature of coffee with an economic lifespan typically up to 30 years (Wintgens, 2004) and the long time required for agroforestry trees to grow to maturity, decisions regarding adaptation to climate change are challenging. Therefore, there is an urgent need for decision support consisting of accurate estimates of climatic suitability for coffee production and the influence of modified microclimate by shade trees, including competition effects (Luedeling et al., 2014). Where long historical records of coffee performance, weather and soil conditions are available, this is a relatively easy task, but the majority of coffee growing areas lack such data (Luedeling et al., 2014). Statistical species distribution modelling approaches (Schroth et al., 2009; Bunn et al., 2015a; Magrach and Ghazoul, 2015) or agro-climatic indices (Lane and Jarvis, 2007) have instead been used. These methods are suitable for characterizing broad agro-ecological zones (Bunn et al., 2015b) and generating hypotheses on the suitable climatic conditions for coffee, but they lack a mechanistic process representation required to predict crop response outside the current growing domain, including the carbon fertilization effect (CFE) induced by rising atmospheric carbon dioxide concentration ($[CO_2]$). Furthermore, while the above studies have analyzed geographical shifts in coffee suitability, indicating a decrease of available area in the future, they did neither include phenotypic responses of the coffee plant (Nicotra et al., 2010) nor management practices allowing for adaptation to climate change, such as shade management, irrigation, or changes in coffee genotypes (Vaast et al., 2016).

Mechanistic crop models are believed to be more appropriate in generating realistic simulations of plant-soil-climate interactions. Moreover, they facilitate learning through hypothesis testing and identification of missing knowledge (Sinclair and Seligman, 1996; Boote et al., 2010), which enables guidance for management action (Harfoot et al., 2014). However, applying such models without sufficient data for calibration, results in large uncertainties of model predictions, next to existing uncertainties in model structure (Beven 2008; Luedeling et al., 2016). The latter is often not identifiable by comparing model outputs with observations alone, as many models can be fitted to the same data leading to the problem of equifinality (Beven and Freer, 2001). Model comparison and critical reflection of assumptions is considered more appropriate (De Kauwe et al., 2014).

Most of the parameters in a crop model are considered “genetic coefficients”, and do not have to be adjusted when applied at different sites (Yin et al., 2004). Yet, some parameters encompass limited process understanding and require calibration when the model is applied to different sites. These include parameters related to the induction of flowering in coffee (Van Oijen et al., 2010b; Rodriguez et al., 2011). Another aspect related to parameter values is phenotypic plasticity, i.e. changes in morphological, chemical, and physical characteristics of a plant in response to the environment. If phenotypic plasticity is explicitly accounted for, there is no need to adapt parameters in different environmental conditions (Yin, 2013). Obviously, this is only possible when the required knowledge is available to adequately represent these processes. Considerable understanding is available on phenotypic responses of coffee to water (Poorter and Nagel, 2000; Carr, 2012; Cavatte et al., 2012; Cannavo et al., 2011) and light availabilities (Matos et al., 2009; Charbonnier et al., 2013; Martins et al., 2014a), but uncertainty is much greater with regard to phenotypic plasticity to atmospheric $[CO_2]$ variation (Yin, 2013), with only few experimental studies regarding coffee so far (Martins et al., 2014c; Ghini et al., 2015; DaMatta et al., 2016).

Other difficulties in exploring possible impacts of climate change on crop production are related to modelling climate extremes and its impacts (Thornton et al., 2014). Depending on the used Global Climate Model (GCM) and the methods for downscaling the output to scales relevant for agriculture, the projected changes in climate may only represent mean changes in temperature and precipitation and not adequately represent changing climate variability, notably temperature and precipitation extremes (Müller et al., 2011; Ramirez-Villegas et al., 2013). In addition to uncertainty in boundary conditions, there is also uncertainty in the actual effects of such extremes on the plant (Reyer et al., 2013).

The goal of this study is to use a mechanistic coffee model, which integrates current knowledge on coffee ecophysiology, to evaluate potential impacts of climate change in various agro-ecological settings and agricultural managements. By making use of statistical approaches to explore the plausible parameter space, we identify optimal current and future management practices of a wide range of potential genotypes. The objectives of this paper are to 1) present the proposed coffee model, 2) assess model outcome in time and space using mean literature derived parameter values, 3) identify model behavior through global sensitivity analysis and 4) evaluate how robust the predicted change is despite parameter uncertainty conditioned by different climate scenarios. We used two contrasting sites of East Africa as case study areas, namely the wet slopes of Mount Elgon, Uganda *vs* the drier slopes of Mount Kilimanjaro, Tanzania.

## 2. Material and methods

### 2.1. Coffee model

The original version of the coffee agroforestry model (CAF2007) was described by Van Oijen et al. (2010b) and extended by Ovalle-Rivera (2014). This study adapts the CAF2014 model for use as a spatially contextualized decision support tool (SpCAF). This model was chosen as it is specifically designed to deal with coffee agroforestry systems and includes a mechanistic light use efficiency approach that deals with the interaction between temperature and $[CO_2]$. In comparison to CAF2014, we assume no nutrient limitations as we intend to isolate the impact of climate on coffee and therefore focus on yield response to water (i.e. water limited yield according to Van Ittersum et al., 2013), temperature and atmospheric $[CO_2]$ levels. Consequently, coffee yield is expressed exclusively as a function of climate and soil water availability, excluding nutrient competition, pest and disease alterations, or allelopathic properties of shade trees on understory coffee. Tree shading is simplified to a canopy that provides shade and competes for water through evapotranspiration. Thus, the objective is not to explicitly model a specific shade tree species, but rather allow for exploration of the continuity between no shade and heavy shade and its effects on microclimate and water competition. The model calculates water-limited coffee yield at a daily time-step and is implemented in R statistics (R Core Team, 2014). In the following sections, all key processes and model assumptions are presented. An overview of the model is illustrated in Fig. 1.

#### 2.1.1. Coffee growth under optimal water supply

Canopy photosynthesis is modelled using a mechanistic light-use efficiency (LUE) approach based on the leaf photosynthesis model of Farquhar et al. (1980) and scaled up to canopy photosynthesis (Charles-Edwards, 1982), as described in detail by Van Oijen et al. (2004). This formula for LUE is calculated on a daily basis and depends on temperature, atmospheric $[CO_2]$ concentration, light intensity and the Rubisco content of upper leaves. Instead of modelling photosynthesis and respiration separately, the LUE approach assumes a constant ratio of daily rates of respiration and photosynthesis, which has been explained experimentally (e.g. Gifford, 1995, 2003) and theoretically (Van Oijen et al., 2010c). The parameters have been adjusted to very low and high light intensity, yielding highest values for LUE at low intensity (Van Oijen et al., 2010b). This allows consistency with observations as reported by Franck and Vaast (2009), Cavatte et al. (2012) and Charbonnier et al. (2017) for Arabica coffee. Moreover, by

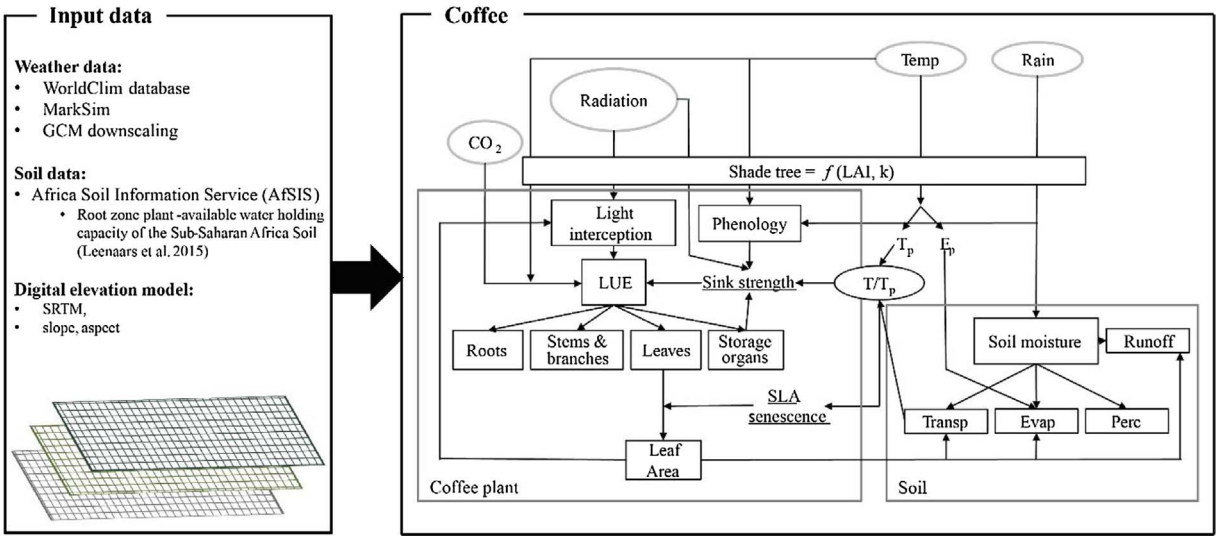


**Fig. 1.** Simplified representation of spatially contextualized coffee growth model.

expressing the LUE approach based on the Farquhar et al. (1980) biochemical model, the interaction between temperature and elevated atmospheric [$CO_2$] is represented (Yin, 2013). Under favorable conditions, growth rate is proportional to the amount of light intercepted by the canopy (Monteith, 1977). Therefore, LUE is multiplied with daily intercepted solar radiation, calculated as an exponential function of leaf area index (LAI) and a constant light extinction coefficient according to Beer's Law for attenuation (Monsi and Saeki, 1953). Water stress decreases LUE proportionally via the ratio of actual to potential transpiration rate (Kropff and van Laar, 1993). The LUE of *C. arabica* has been shown to range between 0.23–0.8 g $MJ^{-1}$ (Bote et al., 2016a; Charbonnier et al., 2017). It has also been shown that LUE can increase by 50% under shade and thereby largely compensate for a reduction in 60% photosynthetically active radiation (PAR) leading to almost equal net primary productivity (Charbonnier et al., 2017). Therefore, using the LUE approach appears to be particularly appropriate for summarizing differences in phenotypic plasticity to shade (Cavatte et al., 2012; Charbonnier et al., 2017; Bote et al., 2016a). This plasticity is reflected by several physiological and morphological adjustments. Firstly, plants in low light conditions allocate more nitrogen to light harvesting rather than carbon-assimilating enzymes (Cavatte et al., 2012; Poorter et al., 2014), although coffee was found to have a robust photosynthetic machinery even in low light that allows to maximize variable light availability by sunflecks (Martins et al., 2013). Secondly, in high light an increased investment in photoprotective mechanisms was observed (Matos et al., 2009). Thirdly, reduced VPD under shade improves stomatal and mesophyll conductance over the day (Franck and Vaast, 2009; Martins et al., 2014b), which is particularly important as coffee photosynthesis is mainly limited by diffusive rather than biochemical limitations (DaMatta et al., 2007; Chaves et al., 2008; Franck and Vaast, 2009; Martins et al., 2014b). Fourthly, increases in specific leaf area (Martins et al., 2014b) and diffuse light availability (Charbonnier et al., 2013) under shade might further increase fraction of absorbed photosynthetically active radiation compared to unshaded systems.

The fraction of carbon (C) allocated to the different plant organs depends on phenological stage (vegetative growth, bean maturation) and is modulated by water availability. Root C sink strength increases with increasing water stress to the detriment of other plant organs according to the functional equilibrium theory (Brouwer, 1983). High fruit load can come at the expense of (i) vegetative growth leading to 'die back' (Vaast et al., 2005) in extreme cases, and (ii) the development of fruiting nodes and hence lower sink strength of fruits in the following year (Vaast et al., 2005; Bote and Jan, 2016). Phenology is based on thermal time (degree days) and flowering is induced by a threshold amount of rainfall after the dry season (DaMatta et al., 2007; Carr, 2012). The intensity of flowering is a function of monthly light intensity around flowering (Cannell, 1985; Franck & Vaast, 2009). Leaf senescence varies depending on the degree of water stress, while roots were set with a constant lifespan. Leaf growth is calculated as the product of leaf biomass and specific leaf area. The latter is decreased by water stress.

### 2.1.2. Soil water balance and water stress

A simple one-layer soil water balance is used to calculate the amount of water in the root zone, whereby water is added by precipitation and lost through interception, transpiration, evaporation, runoff and drainage (Van Keulen, 1986; Van Oijen et al., 2010b). Runoff is calculated as the amount of water lost through surface flow, which is a function of rainfall interception by vegetation cover (modelled by the system's leaf area index), soil water holding capacity, and slope. Drainage is calculated as the remaining water not used by evapotranspiration, interception by vegetation or loss through runoff, which is not retained by the soil (Van Oijen et al., 2010b). No groundwater influence is assumed. Potential transpiration depends on temperature, solar radiation, vapor pressure and LAI and is calculated with the Penman equation (Penman, 1948) according to Van Oijen and Leffelaar (2008). Actual transpiration rate decreases below the potential rate when soil water content is below a critical value, which is lower than field capacity by an amount that depends inversely on atmospheric evaporative demand (Driessen, 1986; Van Oijen et al., 2010b). This critical plant available soil water content additionally depends on the sensitivity of the coffee cultivar to drought. Waterlogging can hamper crop growth when soil water content exceeds a given threshold. Evapo-transpiration demand is partly covered by daily rainfall interception through foliage up to a maximum level which is proportional to LAI (Van Oijen et al., 2010b; Siles et al., 2010).

### 2.1.3. Shade, light transmission, microclimate buffering and water competition

Light transmission through shade tree canopy is modelled with Beer's law using the LAI of the shade tree canopy and an extinction coefficient reflecting different degrees of light transmission and assuming a horizontally homogeneous canopy (Kropff and van Laar, 1993; Zuidema et al., 2005). These two variables allow for varying light transmission through shade tree canopy between 0% and 100%. In reality, the shade tree canopy in agroforestry systems is never homogeneous, and includes multiple layers and species, as well as canopy gaps. Charbonnier et al. (2013) showed that the assumption of a

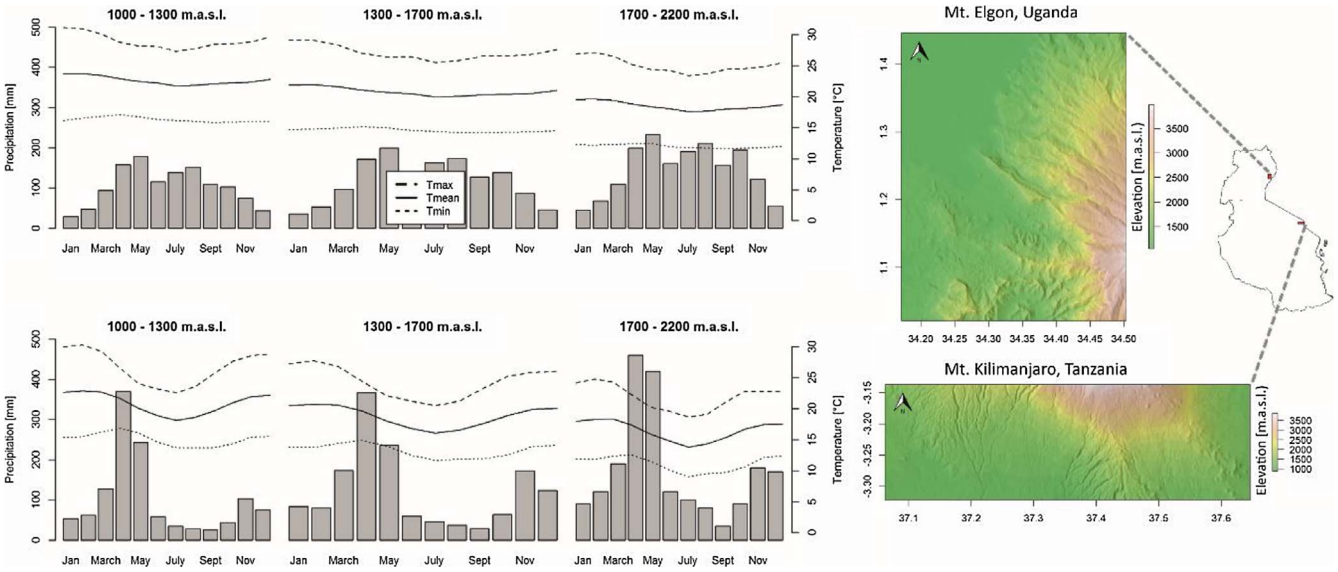


**Fig. 2.** Overview map, digital elevation maps (SRTM; Jarvis et al., 2008) and climate diagrams of Mt. Elgon, Uganda, and Mt. Kilimanjaro, Tanzania, at low (1100–1300 m.a.s.l.), mid (1300–1700 m.a.s.l.), and high altitude (1700–2200 m.a.s.l.) based on the WorldClim database (Hijmans et al., 2005).

homogeneous canopy is nevertheless valid at plot scale, at least under their studied conditions at a humid site in Costa Rica with high planting density of dwarf Caturra variety and low shade tree density with crown projections covering 16% of the farm. Although it is difficult to assume their findings are valid under other environmental and shade management conditions, it is an important indication that plot level modelling might be sufficiently approximated with this approach. Therefore, it provides an appropriate reference for comparing the effects of climate and shade on coffee. Conceptually, non-shaded and homogeneous shade canopy constitute reference points for the extreme shade canopy types, whereby the LAI and light extinction coefficient represent different shade tree compositions. Changes in coffee leaf functional traits (e.g. SLA and leaf nitrogen concentration) between management systems of different vegetation structures (i.e. various shade tree compositions to no shade) is mainly related to light availability rather than shade tree species composition (Gagliardi et al., 2015).

Microclimate modification by shade is reflected as a decrease of daily average temperature proportional to the fraction of radiation intercepted by the shade trees (Van Oijen et al., 2010b). Mean daily temperature decreases according to shade level down to a given maximum (e.g. 4 °C; Beer et al., 1998). Water competition starts with rain interception of shade trees which is proportional to LAI up to a specified threshold (Siles et al., 2010). Tree transpiration was modelled as for coffee with the Penman equation (Penman, 1948). Shade trees transpire water from the same soil-water layer as used by coffee plants. Hence, competition of water occurs when transpiration demands of coffee and shade trees together drive the soil water content below the critical soil water threshold, when actual transpiration rate declines below potential rate.

### 2.2. Climate and soil data

Parameters of the soil-water balance model are retrieved from the gridded functional soil information dataset on root zone plant-available water holding capacity of the Sub-Sahara African Soil (AFSIS; Leenaars et al., 2015). Terrain slope is calculated with the terrain function from the "raster" package (Hijmans, 2015) based on the SRTM 90-m digital elevation model. Daily weather data is generated from the WorldClim database (Hijmans et al., 2005) using the MarkSim weather generator (Jones and Thornton, 2000) on a 30 s resolution (approximately 1 km near the equator) for current (interpolation of observed data, representative of 1950–2000) and future climatic conditions (downscaled GCM data using the delta method (Ramirez-Villegas and Jarvis, 2010) and representative of the 2040–2069 time-slice). Since the objective of this study is to present the model and its behavior instead of a climate change impact assessment, we chose only one GCM to exemplify model capability. We focus the study on possible responses of the coffee plant with consideration of its management to a changing climate, rather than assessing uncertainty in climate change predictions. The Hadley Global Environment Model 2–Earth System (HadGEM2-ES; Jones et al., 2011) from the IPCC 5th assessment report (IPCC, 2013) using the representative concentration pathway 6.0 (Van Vuuren et al., 2011) was chosen for illustration purposes. HadGEM2-ES has been identified as one of the best performing GCMs (e.g Brands et al., 2013; Perez et al., 2014) and is one of the most commonly used. Vapor pressure is estimated from temperature, assuming dew point is equal to minimum temperature as shown by Wang et al. (2004). Solar radiation is estimated with MarkSim using the model of Donatelli and Campbell (1997), cit. in Jones and Thornton, 2000) and adjusted to topography with the 'slopefactor' function of the EcoHydRology package of R (Fuka et al., 2014). Because Arabica coffee is mainly cultivated on the slopes of mountain ranges, spatial resolution should not be too low in order to account for the heterogeneity arising through complex topography. To account for the stochasticity of the MarkSim weather generator, 100 replicates of yearly weather data are simulated for each pixel to account for the diversity of possible weather constellations that monthly mean values could be made up of. We calculated four 25-year growth periods per site and then calculated the mean annual yield values of the 100 year simulations.

### 2.3. Study sites

Two study sites of East Africa were chosen with distinctly different climates (Fig. 2 and Table S1). An altitudinal transect (1000–2200 m.a.s.l.) was selected along the slopes of Mt. Elgon, Uganda, with hot and dry climate at low altitudes, and cool and wet climate at high altitudes. On the other hand, Mt. Kilimanjaro, Tanzania, was chosen as a prominent coffee growing region with severe drought issues and a high predicted climate change impact (Craparo et al., 2015). The precipitation values of the WorldClim data for Mt. Kilimanjaro above 1500 m.a.s.l. were corrected with the insights gained from weather monitoring along the altitudinal transect as recently published by Appelhans et al. (2016), Fig. 4). At the two study sites, the HadGEM2-ES estimates a slightly higher temperature increase and a

lower change in annual rainfall compared to four other commonly used GCMs (Table S2). Therefore, the HadGEM2-ES represents a warmer and drier climate with respect to the other evaluated GCMs. The soils on the slopes of Mt. Elgon and Mt. Kilimanjaro are predominantly Nitisols (WRB for soil classification (IUSS Working Group, 2015), developed on basaltic outflows. Water holding capacity is highly heterogeneous due to the complex topography and is highest at mid altitude (Fig. S1). The selected areas have an extension of 1739 $km^2$ on Mt. Elgon and 1430 $km^2$ on Mt. Kilimanjaro and are important coffee production areas with the majority of households growing coffee. The coffee is often intercropped with banana (*Musa spp*) and a diversity of shade trees with *Cordia Africana, Albizia schimperiana* and *Ficus mucosa* being the most frequent ones (Hemp, 2006; Van der Wolf et al., 2016).

### 2.4. Experimental design

The full continuum of light and water competition was modelled. To calculate optimal shade level per pixel for maximum coffee yield, we varied the shade tree leaf area index between 0 and 3 and the shade tree light extinction coefficient between 0.4 and 0.8, yielding shade levels between 0 and 90%. The continuum of water competition was represented by the two extremes of full potential and no water competition; full potential water competition between coffee and shade trees is assumed due to presence of coffee and tree roots in the same single and homogeneous soil layer and with no preferential access of coffee roots to soil water. For the sensitivity and uncertainty analyses on the other hand, we did not use the full continuum of light and water competition due to high computation demand. We compared non shaded systems with systems covered by 50% shade (shade tree leaf area index = 1 and shade tree light extinction coefficient = 0.7) assuming full water competition.

Climate scenarios consisted of current climatic conditions referring to 1950–2000 according to WorldClim and denoted as year 2000, and future climate representative of the 2040–2069 time-slice (in the following referred to 2050) without elevated atmospheric [$CO_2$] (future A) and with elevated atmospheric [$CO_2$] (future B). Atmospheric [$CO_2$] concentrations for current and future A scenarios were 380 ppm and 478 ppm for future B scenario, according to the IPCC representative concentration pathways (RCP) 6.0 (Van Vuuren et al., 2011). For the future B scenario, we assumed neither photosynthetic downregulation nor changes in carbon allocation to represent the maximum possible $CO_2$ fertilization effect (CFE). The future A scenario represents the "temperature" effect of climate change, and the difference between future B and future A, represents the uncertainty in CFE. Maximum CFE reflects increased photosynthesis and water use efficiency assuming no phenotypic responses to elevated [$CO_2$]. The uncertainty range, therefore, reflects possible physiological and/or morphological changes as a response to elevated [$CO_2$] not accounted for by the model. For the sensitivity analysis and prior (i.e. uncalibrated) uncertainty assessment, we chose two locations each on Mt. Elgon and Mt. Kilimanjaro, one at low altitude (1097 and 1133 m.a.s.l., respectively) and a second one at high altitude (1863 and 1629 m.a.s.l, respectively).

### 2.5. Evaluation

#### 2.5.1. Parameter ranges and assumptions

Parameter ranges were selected as marginally uniform distributions based on published studies as presented by Van Oijen et al. (2010a) and from more recent literature (see Table S3 and S5). It is important to differentiate between parameter values that can be considered as generally valid for all Arabica coffee species and parameter values that are genotype specific (Boote et al., 2003). Genotype specific parameters include carbon allocation parameters, transpiration coefficient, light extinction coefficient, leaf Rubisco content, time between seedling planting and reproductive phase, specific leaf area, and parameters of plant organ senescence. Differences between traditional low yielding and improved high yielding genotypes can be largely explained by differences in carbon allocation patterns, whereby the efficiency of the photosynthetic apparatus remained almost the same (Génard et al., 2008; Ericsson et al., 1996). For example, the difference at juvenile stage between the coffee cultivars *Coffea arabica* cv. Caturra, Catuai, and Catimor was mainly related to morphological variables (i.e. height, leaf area, internode number, root to shoot ratio), while physiological variables (i.e. leaf net photosynthetic rate, stomatal conductance, intercellular [$CO_2$], and intrinsic water-use efficiency) were not significantly different (Zhang et al., 2017).

#### 2.5.2. Sensitivity analysis

A global sensitivity analysis was performed using the extended Fourier amplitude sensitivity test (eFAST) of Saltelli et al. (1999). The eFAST estimates the contribution of individual input factors to output variance and evaluates the variability of the output for the entire uncertainty domains of the parameters. Additionally, it addresses higher-order interaction between input factors. The method makes use of a sampling approach following a systematic search trajectory designed to explore the parameter space via a transformation function. A first-order sensitivity and a total-effect sensitivity index are computed from the generated trajectories using a spectral decomposition of the model output variability. The total output variance is decomposed to estimate the influence of individual parameters by its main effects and the interactions with other parameters. This method was shown to be more efficient than Sobol's method (Sobol', 1993) which uses a Monte Carlo approach to estimate first and total sensitivity indices (Makowski et al., 2006) and has been shown to be more robust than several other global sensitivity methods (Chan et al., 1997; Saltelli and Bolado, 1998). Furthermore, computational demand is significantly lower with eFAST and interaction effects among parameters are computed, which is not the case with Sobol's algorithm. We used the sensitivity R package by Pujol et al., (2015). Conversion of the sensitivity indices was found for a sample size of factor 1000 resulting in 26 000 model runs with 26 parameters, i.e. 26 000 parameter vectors were sampled and run with the model per climate and management scenario.

### 2.6. Prior parameter uncertainty analysis

As the exact parameter values are unknown, we evaluate how the different shade management and climate scenarios impact on the different parameter sets within the range of parameter uncertainty. This approach is called forward uncertainty analysis (Beven, 2008), as the outputs depend entirely on the prior assumptions of the parameters, which are propagated forward through the model predictions. To assess forward parameter uncertainty, we use the parameter vectors as sampled with the eFAST method. The uncertainty is exemplified for a hypothetical but realistic (i.e. derived from existing literature) coffee Arabica genotype. Therefore, we set the light extinction coefficient and Rubisco content in leaves to 0.65 ($m^2\,m^{-2}$) and 0.54 ($g\,m^{-2}$), respectively. The uncertain parameters are given in table S4. The soil parameters representing the fraction of water content at field capacity, air dryness, wilting point, and water saturation have been set to the values of the respective pixels of the AFSIS database (Leenaars et al., 2015).

## 3. Results

### 3.1. Model runs with mean parameter values

#### 3.1.1. Mount Elgon

On Mt. Elgon, the high altitude is currently the most suitable area for coffee production with a peak at 1780 m.a.s.l. (Fig. 3). Due to the optimal mean annual temperature (19.3 °C), annual precipitation (1654 mm), high cloud cover and hence low daily mean solar radiation (19.7 $MJ\,m^{-2}\,d^{-1}$), coffee is not dependent on shade for buffering microclimate. Shade becomes beneficial from 1500 m.a.s.l. on

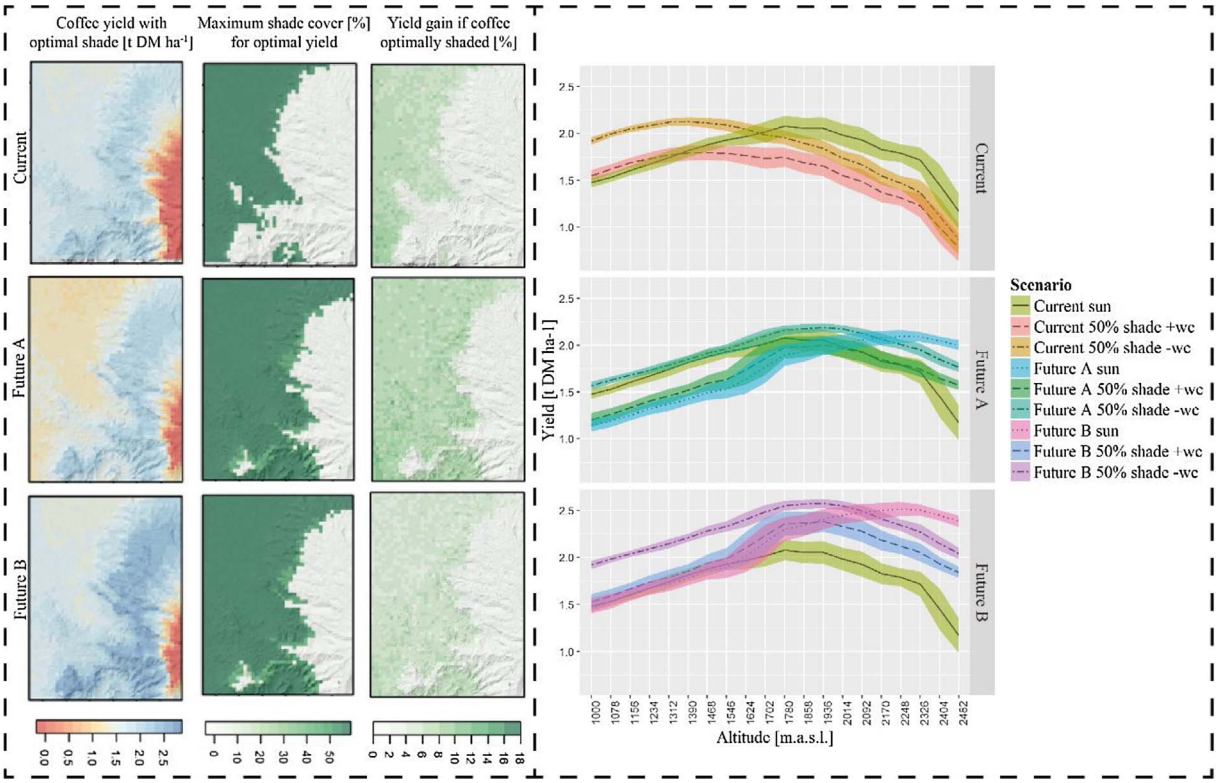


**Fig. 3.** Mapped rain-fed coffee yield with optimal shade on North-Western slopes of Mt. Elgon, Uganda. First row refers to current climate (baseline: 2000), second and third rows refer to future (2050) climate without (future A) and with (future B) CFE, respectively. First column refers to rain-fed yield with optimal shade level [t DM ha-1], second column to maximum canopy cover [%] allowing for maximum yield, third column refers to yield gain if system optimally shaded *vs*. no shade with full potential water competition [%]. Future A and future B represent minimum and maximum magnitude of CFE, respectively. Shade + wc and − wc refer to full potential and no water competition (wc), respectively. On the right side of the maps are the altitude profiles of the respective scenarios of mean coffee yield with standard deviation.

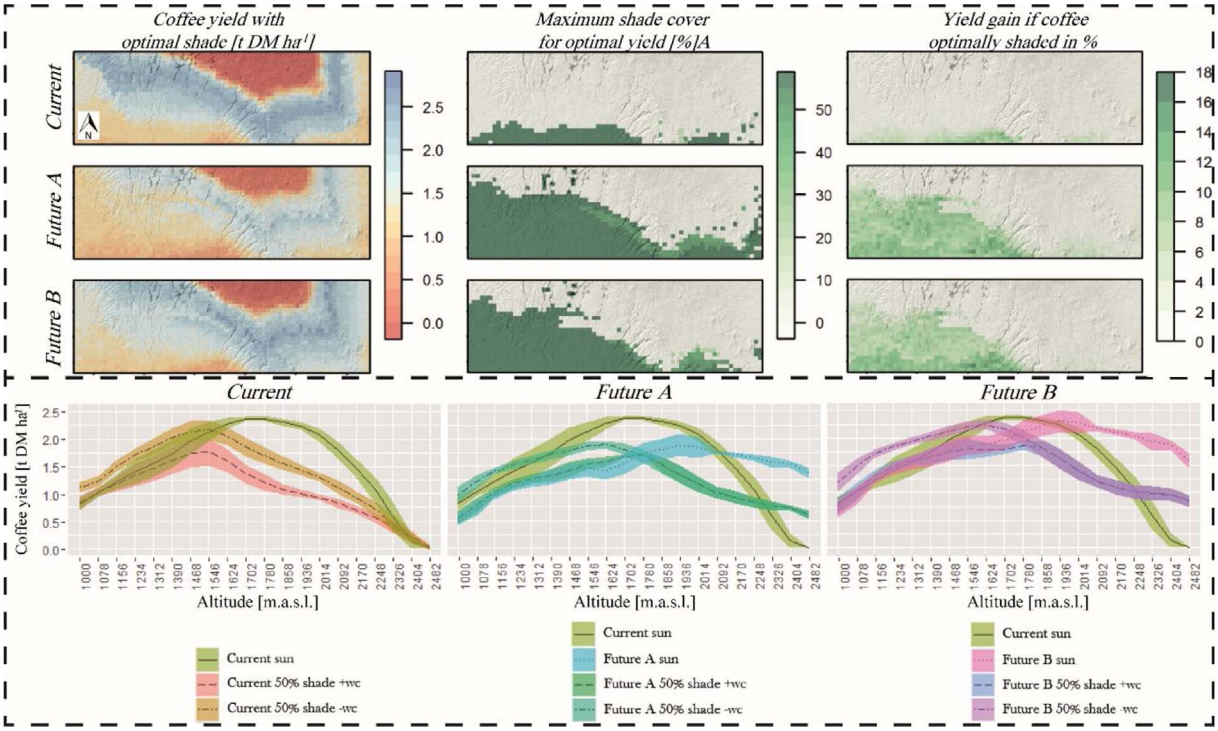
Coffee yield with optimal shade [t DM ha-1]
Maximum shade cover for optimal yield [%]A
Yield gain if coffee optimally shaded in %
Current
Future A
Future B
Coffee yield [t DM ha-1]
Altitude [m.a.s.l.]
Current sun
Current 50% shade +wc
Current 50% shade -wc
Future A sun
Future A 50% shade +wc
Future A 50% shade -wc
Future B sun
Future B 50% shade +wc
Future B 50% shade -wc

**Fig. 4.** Mapped rain-fed coffee yield with optimal shade on Southern slopes of Mt. Kilimanjaro, Tanzania. Upper dashed box: First row refers to current climate (baseline: 2000), second and third column refer to future (2050) climate without (future A) and with (future B) CFE, respectively. First column refers to rain-fed yield with optimal shading [t DM ha-1], second column to maximum canopy cover [%] for maximum yield, third column refers to yield gain if system optimally shaded *vs*. no shade with full potential water competition [%]. Future A and future B represent minimum and maximum magnitude of CFE, respectively. Shade + wc and − wc refer to full potential and no water competition (wc), respectively. Lower dashed box illustrates the altitude profiles for the different scenarios of mean coffee yield with standard deviation.

downwards, whereby the benefit increases as altitude decreases. Maximum yield gain due to optimal shade management assuming full potential water competition is 11% for current and 13% and 10% for future A and B, respectively. At low altitude, shade up to 50% increases coffee yield, despite the conservative assumption of non-preferential access of coffee roots to soil water and hence full potential water competition between coffee and shade trees. Yet, some areas at low altitudes have soils with low water holding capacity resulting in increased competition for water between coffee and shade trees. In the scenario of future climate (2050) as predicted by the HadGEM2-ES without considering elevated atmospheric [$CO_2$], coffee yield is negatively affected up to 2000 m.a.s.l., with a maximum decrease of 44% on poor soils at low altitude (mean = −25%), while at altitudes higher than 2000 m.a.s.l. yield is increased due to predicted higher temperatures. Optimal coffee suitability increases up to 2200 m.a.s.l. equaling an altitudinal shift of 400 m; this drastically reduces the suitable area for coffee cultivation as exemplified by a comparison of maps on current and future A scenarios (Fig. 3). The increased yield in the future, limited to the highest altitudes, is additionally attributed to a foreseen precipitation increase [100–300 mm $yr^{-1}$]. However, this area coincides with the protected Afromontane forest starting at around 2200 m.a.s.l., hence agricultural expansion to these higher altitudes is not permitted. Shade as an adaptation strategy allows to adapt currently non-shaded systems in the future but only if coffee is associated with tree species not competitive but rather complementary in terms of water use. Unless water competition is adequately dealt with, the benefit of modified microclimate by shade trees will not be able to sustain the current yield level. Assuming no phenotypic plasticity as a response to elevated [$CO_2$], the CFE cancels the negative effect of high temperature at low and mid altitudes on Mt. Elgon, while at high altitude yield is increased [10–15%].

#### 3.1.2. Mount Kilimanjaro

On the slopes of Mt. Kilimanjaro, the highest yield of rain-fed coffee is between 1600 and 1800 m.a.s.l. (Fig. 4). Shade improves coffee yield at lower altitudes ( < 1600 m.a.s.l.) only if non-water-competitive shade tree species are used. Assuming full potential water competition, shade is beneficial solely up to 1370 m.a.s.l., due to the dry climate reducing the net benefit of shade trees. Furthermore, the temperature effect of predicted climate change, according to the HadGEM2-ES without considering elevated [$CO_2$], decreases yield up to 1730 m.a.s.l. Higher evaporative demand and hence water stress will be a serious problem and the issue of water competition between coffee and shade trees even more critical. Adapting coffee systems to this foreseen climate will require substantial knowledge on shade tree selection and management. Elevated [$CO_2$] might mitigate the negative effects of predicted climate change at low altitude if no physiological and/or morphological acclimation processes take place. At mid altitude, future elevated [$CO_2$] conditions will not be able to maintain the same yield levels as under current conditions. Maximum yield gain with optimal shade management assuming full potential water competition is 12% for current and 18% and 17% for future A and B, respectively.

### 3.2. Prior parameter uncertainty

Prior parameter uncertainty analysis provides insights on the qualitative changes to be expected using different parameter sets when evaluating different shade management and climate scenarios (Fig. 5). The mean responses of the impact of different management practices (no shade *vs*. shaded systems) at current and future (with CFE *vs* no CFE) climatic conditions over a longer time period, give a clear picture of the climate signal. Incorporating shade trees with 50% canopy cover at low altitude (1092 m.a.s.l) on Mt. Elgon benefits coffee yield on average by 13.5% over a 25 year growth period, despite high parameter uncertainty (Fig. 5). This shade level also constitutes the optimal shade level for highest coffee yield (Fig. 6). A few parameter sets reveal no change or even a yield decrease under shaded conditions. This occurs under conditions of combined low leaf sink strength, low maximum leaf life-span, and short thermal time requirement for bean maturation. Such a parameter constellation is unlikely present in a real genotype, therefore making this scenario rather unrealistic. Yet, to improve our model understanding it is still helpful to identify such conditions. In these parameter constellations, LAI is too small to adapt to the limited light availability under shade, which outweighs the benefits of improved microclimate. Furthermore, the short thermal time requirement for bean maturation, results in an increased photo-assimilate demand by berries that cannot be provided by the low leaf area and low light availability. At high altitudes, on the other hand, shade with 50% canopy cover is not beneficial for coffee yield compared to unshaded systems (Fig. 5), due to the already low temperature, high humidity associated to high annual rainfall, and low solar radiation due to high cloud cover. None of the evaluated parameter constellations allow for improved yield under shade at high altitude. Unshaded coffee outperforms shaded coffee in terms of coffee yield at current climatic conditions at high altitude (Fig. 6).

In a future climate as projected by the HadGEM2-ES, coffee yield is hampered by increased temperature and drought stress at low altitude (-18%) if no elevated atmospheric [$CO_2$] concentration is assumed (Fig. 5). For most parameter constellations, this negative impact on yield can be mitigated if shade is included allowing to maintain current yield in the future. A shade level of 50% continues to provide the highest net benefit resulting in highest yield (Fig. 6). The shade effect for different parameter constellations has been described above. In a future scenario with elevated atmospheric [$CO_2$] reaching 478 ppm, the negative impact of increased temperature and drought stress is mitigated (Fig. 5), allowing to maintain current yield in the future even without shade. This is assuming neither a downregulation in photosynthesis nor changes in carbon allocation as a response to elevated [$CO_2$]. As shown in Fig. 5 and 6, optimizing shade management under these conditions results in increased yield compared to current unshaded systems (18%). At high altitude, by contrast, increased temperatures will benefit coffee yield in both scenarios (no/with elevated [$CO_2$]). Shade with 50% canopy cover at these altitudes will not be able to outperform unshaded systems either today or in the future, if the sole objective is to maximize coffee yield (Fig. 5). But shade up to 18% does not lead to a yield reduction (Fig. 6).

On Mt. Kilimanjaro, Tanzania, shade also improves coffee yield at low altitude (24%) but not at high altitude. Compared to Mt. Elgon, future predicted climate change has a more negative effect in both scenarios, without (-32%) and with elevated [$CO_2$] (-18%) in unshaded conditions. But yield can be improved by shading to (-2%) and (16%) in scenarios without and with elevated [$CO_2$], respectively. Although shading coffee at high altitude reduces potential yield at current climatic conditions, it buffers coffee systems against future climate scenarios and helps maintain yield (no elevated [$CO_2$]) or even increases yield (with elevated [$CO_2$]).

### 3.3. Parameter sensitivity

The most sensitive parameters are those related to soil water availability (i.e. amount of water available for coffee and trees between field capacity and wilting point), light interception (light extinction coefficient), photosynthesis (Rubisco content in leaves), and carbon allocation (i.e. sink strength for leaves and storage organs) (Fig. 7). These parameters need to be well known or appropriately estimated to reduce uncertainty. The remaining parameters do not significantly influence output variance and hence can be set as constant values allowing for model simplification. The difference in parameter sensitivity to changes in environment (Uganda *vs* Tanzania/low *vs* high altitude) is less than to shade level.

Shade reduces the energy input reaching the soil and the coffee plants, and therefore reduces water use by coffee transpiration and to a

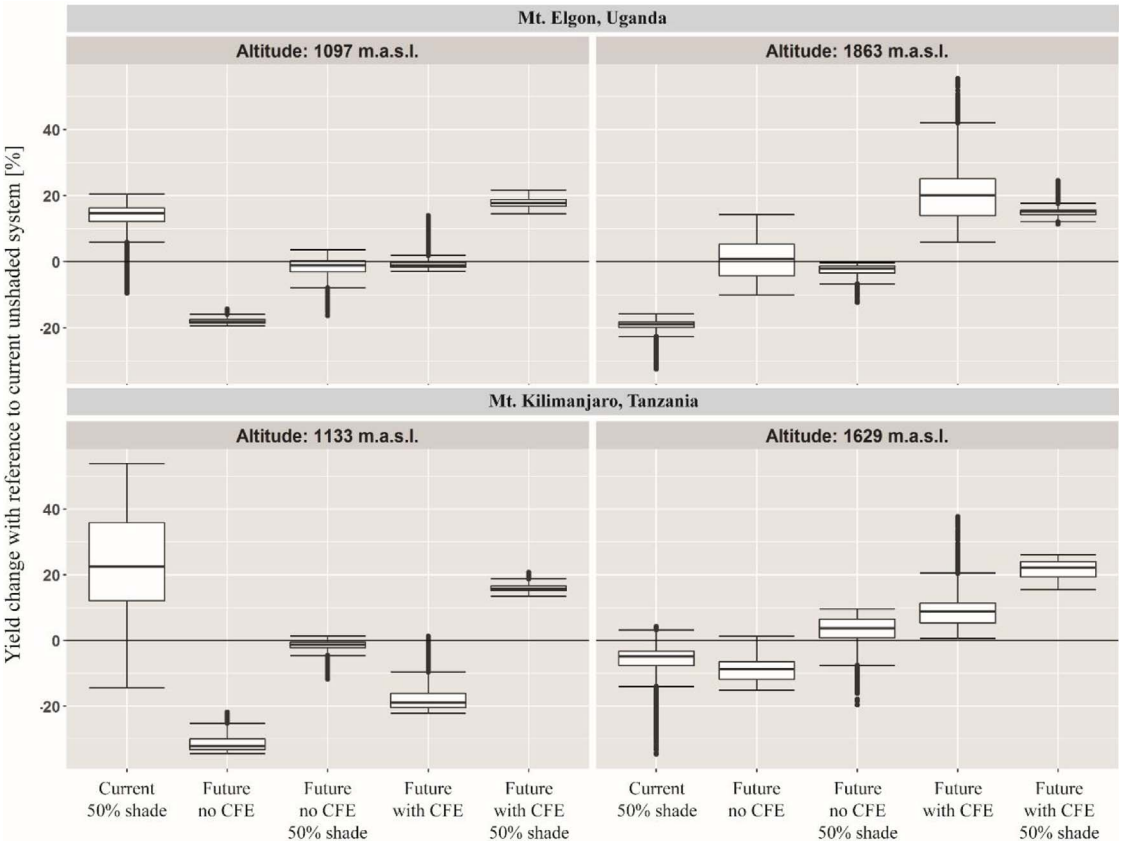


**Fig. 5.** The relative coffee yield change due to the HadGEM2-ES climate change scenario, with and without [CO2]-fertilization effect (CFE) and with 0 or 50% shading of shade trees on low and high altitude of Mt. Elgon, Uganda and Mt. Kilimanjaro, Tanzania, including the prior parameter uncertainty.

lesser extent soil evaporation. Yet, adding transpiration of the shade trees, hence assuming full potential water competition all year around, leads to high sensitivity of soil parameters. The soil water budget of coffee plants is less important under shaded conditions when there is no water competition. The strong influence of soil hydraulic parameters (parameters related to field capacity and wilting point) highlights the need for using high quality soil data as inputs. As water becomes less limiting, parameters related to light interception, canopy photosynthesis, and carbon allocation become more important. The C sink strength of roots gains importance in water limited conditions when soil hydraulic parameters are excluded of the sensitivity analysis (data not shown), while sink strengths of leaves and berries are relatively more important in light limited conditions.

As shown in Fig. 7, the general pattern of model parameter sensitivity between Mt. Elgon and Mt. Kilimanjaro is consistent, despite the differences in climatic conditions. The main difference is the higher sensitivity of parameters related to thermal time, namely base temperature for maturation (TMATB) and thermal time to maturation (TMATT) particularly in unshaded systems located at low altitude.

The soil water balance parameters are provided as input by the AFSIS database, whereby the uncertainty of this database is not considered in this study. Yet, as the model is very sensitive to soil hydraulic

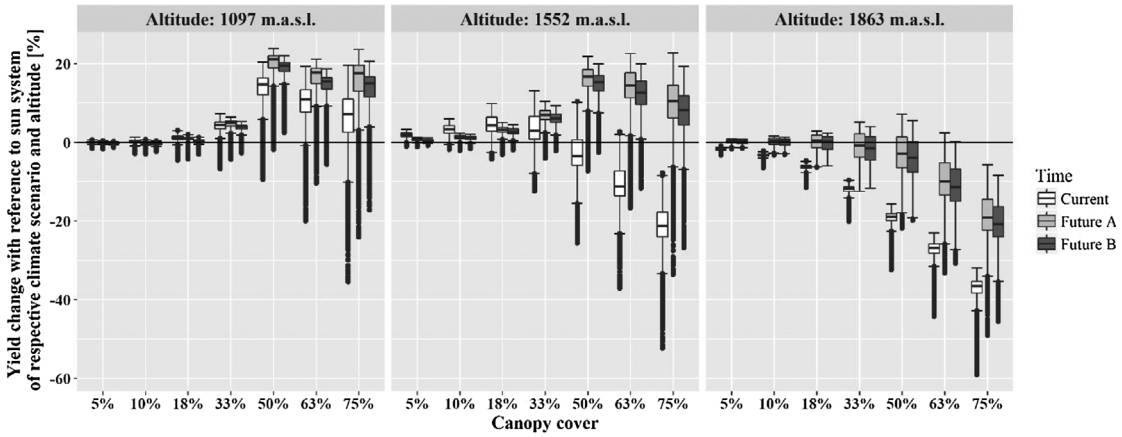


**Fig. 6.** The relative benefit of shade on coffee yields per climate scenario (without reference between climate scenarios) compared to non-shaded systems of the three climate scenarios on Mt. Elgon, Uganda, including prior parameter uncertainty. These responses assume full potential water competition between coffee and shade trees. The reference zero line represents either current sun system, future A sun system (assuming no [CO2]-fertilization effect), or future B sun system (assuming [CO2]-fertilization effect without change in phenotypic plasticity), respectively (and thus is different to that in Fig. 5).

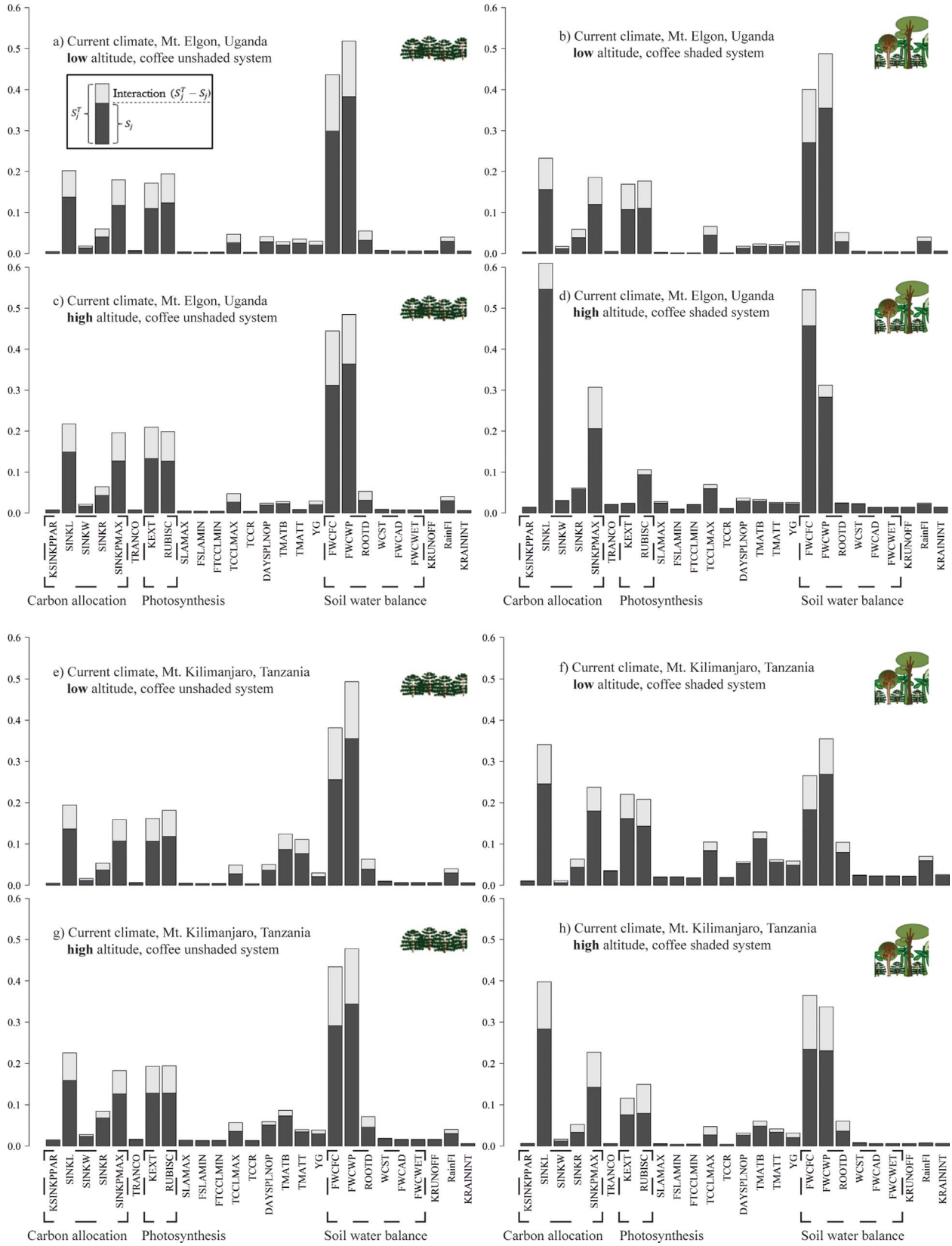


**Fig. 7.** The first-order and total-effect sensitivity indices for model parameters of different climatic conditions (low *vs* high altitude) and different shading regimes (no shade *vs* 50% shade). Description of parameters is provided in Table S3.

parameters, accurate estimates are required to reduce uncertainty. For calibration purposes, it is important to know which parameters are critical when removing them from the analysis. When excluding the soil water balance parameters, the sensitive parameters ($> 0.1$) are (in descending order): carbon sink strength of leaves (SINKL), Rubisco content of upper leaves (RUBISC), sink strength for storage organs (SINKPMAX), light extinction coefficient (KEXT), and carbon sink strength of roots (SINKR).

## 4. Discussion

We presented a model that allows to taking into account spatially-explicit soil and climate characteristics to explore management options for coffee systems via shade tree association. One GCM was used, as the main purpose of this study is the presentation of the model features rather than a full climate change impact assessment. Nonetheless, consistent with earlier studies, we found negative impacts of increased temperature at low altitude, while high altitude areas should gain in terms of yield potential (Bunn et al., 2015a; Magrach and Ghazoul, 2015). Our model suggests that the CFE could potentially mitigate the negative effects of increased temperature to a large extent, hence suggesting that previous studies might have overestimated the negative impact of climate change. Additionally, one of the most salient features of the present model is to calculate the optimal shade level along environmental gradients now and in the future according to different climate scenarios. Below we discuss differences among coffee genotypes, the effect of shade and [$CO_2$] fertilization, the importance of soil water availability, the interaction between temperature and [$CO_2$] effect, as well as implications for smallholders on Mt. Elgon and Mt. Kilimanjaro, and ultimately model improvements.

### 4.1. Genotypic variation

Data availability for calibration purposes is a major constraint. Explicitly analyzing the uncertainty range in parameters is therefore of great importance (Beven, 2008). Due to the lack of certainty concerning which parameter sets best simulate the actual genotypes and planting densities currently cultivated at the sites of interest, we did our simulations based on the entire range of parameter values by sampling the plausible parameter space. Despite the uncertainty in the absolute change induced by the assessed scenarios compared to current non-shaded systems (Fig. 5 and 6), the model allows for identifying the direction of change in coffee yield (Reyer et al., 2016). It further exemplifies the potential of improved genotypes in the context of climate change adaptation (Bertrand et al., 2016). The maps in Figs. 3 and 4 represent only one general Arabica genotype at a fixed planting density resulting in relatively low observed water-limited yield up to 2.5 t/ha. The use of modern high yielding dwarf varieties (e.g. Catimor derived varieties) planted at high density (4000–5000 plants/ha) as commonly found on coffee plantations in Brazil and Colombia, for example, can reach yield levels over 3 t/ha (Van der Vossen, 2005; DaMatta et al., 2007). Different coffee varieties exhibit different yield potentials and responses to environmental stresses. Differences in morphological traits have been identified to be the main determinants of yield differences and drought tolerance among Arabica cultivars (Tausend et al., 2000; Zhang et al., 2017). Open questions remain regarding genotypic differences in temperature tolerance and response to elevated [$CO_2$]. Furthermore, hybrid varieties between Arabica, Robusta and hybrids of Timor have been developed mainly for pest and/or disease resistance (Bertrand et al., 2016; Herrera and Lambot, 2017) that could potentially also benefit of Robusta's tolerance to higher temperature. To analyze this, data of different varieties on the physiological (particularly stomatal conductance) and morphological characteristics are required. The sensitivity analysis (Fig. 7) highlights that plant architecture (light extinction coefficient) plays an important role in plant performance under shaded or non-shaded conditions. Traditional varieties which have a less dense canopy (Unigarro et al., 2016) are usually better adapted to shade, while modern dwarf varieties with high self-shading often grow well without shade (Montagnon et al., 2012). Genotypic differences regarding responses to light availability are of great interest for using agroforestry systems as adaptation strategy (Bertrand et al., 2016).

### 4.2. Effect of shade

The model allows for estimating the optimal shade level along environmental gradients now and in changing future climates. In areas with optimal water supply, elevated temperatures and high solar radiation, a range of shade tree species can be used with beneficial effects for coffee yield. In these areas, trees with high timber value or fast-growing ones can substantially improve farmers' livelihoods (Schaller et al., 2003; Vaast et al., 2008; Vaast et al., 2015). Where water is limiting, shade trees need to be selected with high root niche differentiation (Cannavo et al., 2011; Padovan et al., 2015) and non-competing phenology. The latter also provides options to optimize light availability (Beer et al., 1998). Knowledge of appropriate selection of shade tree species (Van der Wolf et al., 2016) and their management related to timing and amount of pruning is thus required (Beer et al., 1998). It is important to further consider the economic impact of agroforestry systems. At locations where shade does not decrease coffee yield, or when such decreases are relatively small, increased farm profitability and revenue diversification can be achieved by farmers due to the co-production of other agroforestry products, such as fruits, firewood, and timber (Rice, 2011; Vaast et al., 2015).

We showed that the model responds well to decreasing light availability, by increasing the sensitivity of parameters relevant to light interception (Fig. 7). Soil hydraulic parameters had a strong effect on yield, which emphasizes the importance of sound soil input data. Different soil types will therefore have an important influence on yield output, which need to be accounted for in addition to changes in climate variables. We suggest the use of recently established spatial databases on root zone plant-available water holding capacity (Leenaars et al., 2015), but uncertainties in these data should be taken into account in future studies. These soil types in combination with precipitation regime and root distribution of shade tree species will largely determine the risk for water competition or potential for complementarity between coffee and intercrops/shade trees (Van Kanten and Vaast, 2006; Cannavo et al., 2011; Padovan et al., 2015).

In this study, light and water competitions were estimated conservatively, assuming homogeneous shade cover and full potential water competition within a single soil layer. Nevertheless, the selected approach allows the calculation of the biophysical determinants of successful agroforestry systems (Sanchez, 1995) at the critical endpoints of the continuum of different degrees of light and water competition. Shade tree species differ substantially in the way they intercept light and use water based on their canopy, root architecture and phenology (e.g. deciduous vs. evergreen trees) (Luedeling et al., 2016). On the other hand, the model does not account for the effect of shade and climate change on pests and diseases. Shade can either have beneficial or negative effects on pests and diseases depending on environmental context (Jonsson et al., 2015; Liebig et al., 2016) which additionally requires careful consideration for shade tree management (Staver et al., 2001).

### 4.3. Effect of [$CO_2$] fertilization

We identified that an increase in [$CO_2$] might substantially mitigate some of the negative impacts caused by climate change, although the magnitude of that mitigation effect is not clear due to possible responses in phenotypic plasticity (Aspinwall et al., 2015). To account for this uncertainty in CFE, we modelled zero effect (modelled by omitting an increase in [$CO_2$] in the future) and the effect resulting when no

phenotypic plasticity is assumed as a response to elevated [$CO_2$] from 380 ppm to 478 ppm. The model indicates an averaged maximum effect on coffee yield between 13.5–21% (Fig. 5), with higher effect at the more humid Mt. Elgon site, compared to the drier Mt. Kilimanjaro site. Although water-use efficiency generally increases due to elevated [$CO_2$] at an instantaneous time-scale, the duration of stomatal opening at longer time scales is increased at more humid sites which can lead to higher overall benefit of [$CO_2$]. Our modelled values agree well with the average response of 13% found in free-air [$CO_2$] enrichment experiments (FACE) across a range of $C_3$ crops (Long et al., 2006) and a recent one conducted on coffee in Brazil, resulting in a yield increase of 12.0–14.6%, depending on genotype, due to increasing atmospheric [$CO_2$] concentrations from 390 ppm to 550 ppm over a two-year period without increasing ambient temperature (Ghini et al., 2015; DaMatta et al., 2016). This yield increase was even larger (approx. 40%) in the third year leading to a mean increase of 28% (Raquel Ghini, personal communication). This high CFE found in this FACE experiment is due to the absence of downregulation in photosynthetic capacity or acclimation of stomatal conductance. There was no decrease in leaf nitrogen content and no alteration in leaf Rubisco content. Differences between the two evaluated genotypes in their responses to elevated [$CO_2$] were found, suggesting some uncertainties on how other common Arabica varieties might respond. Anyway, this general lack of phenotypic plasticity in response to elevated [$CO_2$] is exceptional when compared to many other $C_3$ plants (Ainsworth and Long, 2005) and suggests that Arabica coffee benefits comparatively well from CFE. This appears to be due to the fact that coffee photosynthesis is highly limited by diffusional rather than biochemical limitations (Martins et al., 2014b). Research on other $C_3$ plants with similar diffusional limitations have also indicated above-average benefit of CFE (Niinemets et al., 2011; Flexas et al., 2014). Additionally, as a perennial woody species it has a larger carbon sink capacity compared to annual crops (Ainsworth & Long, 2005). Higher water use efficiency is achieved by increasing net photosynthesis at maintained stomatal and mesophyll conductance (DaMatta et al., 2016). Maintaining stomatal conductance is beneficial as a reduction might result in an increased leaf temperature via its effects on leaf energy balance (Bernacchi et al., 2007), which could exacerbate the warming induced by climate change.

### 4.4. Interaction between temperature and [$CO_2$] effect

To what extent elevated [$CO_2$] might mitigate increased temperature is unclear and might be different for different genotypes and dependent on the accompanying change in air humidity and soil water availability. Growth chamber studies have found increased tolerance of coffee to supra-optimal temperature at elevated [$CO_2$], mainly due to increased investment into protective measures (Martins et al., 2016; Rodrigues et al., 2016). The degree of this increased tolerance will depend on the temperature and precipitation induced changes in soil moisture and VPD and the vigor of the coffee plant. Therefore, hot and humid areas are expected to benefit more from the interaction between elevated [$CO_2$] and supra-optimal temperature, compared to areas that will become hot and dry. This explains why our model implies that elevated [$CO_2$] does not allow to maintain current yield on Mt. Kilimanjaro, while on Mt. Elgon it might cancel out the negative effect of increased mean temperature. Irrigation practices are widespread in the Kilimanjaro area (Hemp, 2006) and the last two decades (1990–2010) have been identified as quite dry compared to average climate, with reductions in precipitations during the main growing season (Otte et al., 2016). Further drying is projected by the HadGEM2-ES due to decreased rainfall in combination with higher evaporative demand as a result of higher temperatures, particularly during bean filling. This likely results in increased C demand for maintenance and respiration as well as for bean filling, with simultaneous decrease in photosynthesis due to increased VPD and drought stress. Importantly, we have to be aware that there remain high uncertainties on how the interactions between warming and elevated [$CO_2$] will impact flowering, bean maturation and cup quality. For example, there are indications that flowering might be severely reduced under increased temperature (Drinnan and Menzel, 1995; Craparo et al., 2015), which is currently not included in the model due to limited process knowledge. Pest and disease pressure will additionally change and likely continue to constitute a primary production constraint to coffee cultivation, for which we have only limited information at present (Jaramillo et al., 2011; Ghini et al., 2015; Jonsson et al., 2015).

### 4.5. What does the [$CO_2$] effect mean for smallholder farmers on Mt. Elgon and Mt. Kilimanjaro?

The vast majority of farmers on Mt. Elgon and Mt. Kilimanjaro are smallholders, who face several constraints to access adequate nutrient and pest and disease management options, leading to coffee systems with very low yield (Wang et al., 2015; Craparo et al., 2015; Liebig et al., 2016). Therefore, it is unlikely that they will benefit of the CFE, unless appropriate actions to promote climate-smart agricultural management are taken (Vaast et al., 2016). The challenge of the CFE is that it favors highly intensified systems, thereby further increasing their competitive advantage compared to extensive ones of smallholders, and hence likely making the formers more vulnerable (Morton, 2007). The opportunity of CFE, however, is that improving smallholders' farming conditions might allow more of them to continue cultivating coffee in the future than previously estimated.

### 4.6. Model improvements

Several aspects need to be highlighted for future improvements regarding the present coffee model. Firstly, further insights are required on how coffee light use efficiency is affected by different light availabilities at different time scales. This allows for clarifying to what extent the mechanistic light use efficiency approach (Van Oijen et al., 2004) is an appropriate summary model of changes in microclimate due to shade (i.e. changes in minimum and maximum temperatures, decreased VPD and increased diffuse light) and changes in phenotypic plasticity of the coffee plant. Secondly, we still lack a sufficient mechanistic understanding of flowering induction and associated asynchronous flowering events. A first attempt has been done by Rodriguez et al. (2011) by using demographic population models which should be further evaluated. To improve our understanding, it will require long term data sets of flowering events combined with weather and soil data of different environmental contexts. The same is required to better understand factors leading to flower abortion. Thirdly, a more detailed modelling routine might be required for branch dynamics that adequately represent competition between fruit load and increment in branch and new branch development. Depending on the new branches formed and extension of existing branches, the nodes and potential flowering should be calculated. Finally, improvement is also required in representing the impact of extreme events, such as temperature and rainfall, on coffee productivity. As more data become available, more complex process representation will be possible, either through direct parameterization or inverse modelling. Particularly, this is needed for extending the soil water balance to multilayered soil compartments enabling root niche differentiation between the coffee plant and shade trees as recently exemplified in Nicaragua (Padovan et al., 2015). In order to better account for differences in canopy structure of the shade trees, summary models as presented by Duursma and Mäkelä (2007) and Forrester (2014) could be implemented, with intermediary complexity between our present approach and the MAESTRA approach as used by Charbonnier et al. (2013, 2017).

These improvements strongly depend on data availability. The collection of functional trait data for different genotypes in different environmental contexts will allow to analyze genotypic and phenotypic plasticity and significantly contribute to the required data for modelling

endeavors. This requires the consolidation of available functional trait data for coffee (particularly flowering phenology) and shade trees within the plant trait database (Kattge et al., 2011; Martin and Isaac, 2015) but also on coffee yield, management practices and local knowledge (Ordonez et al., 2014; Van der Wolf et al., 2016). Consolidation of such a database would improve either direct parameterization or calibration through inverse modelling, for example by using a Bayesian approach, thereby allowing to estimate parameter values in different climates where weather, soil and production data are available (Van Oijen et al., 2005).

## 5. Conclusions

We presented a mechanistic model that processes spatially-explicit soil and climate data to guide coffee cultivation and shade tree management for sustainable coffee production systems. We applied the model to two case studies, namely the slopes of Mt. Elgon, Uganda, and Mt. Kilimanjaro, Tanzania. According to the GCM used (HadGEM2-ES), Mt. Kilimanjaro will be severely affected by a drying climate in the future, while Mt. Elgon is impacted to a lesser extent. The presented modelling results confirm earlier studies on coffee suitability changes, namely that low-altitude areas will be more strongly affected by climate change. However, previous studies did not include neither CFE nor shade management and consequently seem to have overestimated the negative effects of mean changes in temperature and shifts in precipitation regimes; i.e. yield improvements due to elevated [$CO_2$] seem to largely mitigate the negative impacts of elevated temperature. Shade trees can play a strong beneficial role at the low-altitude areas that have more marginal climates and will suffer most from climate change. Higher altitude areas ($> 1500$ m) may see little to no direct benefit from shade trees on coffee yield. The model outputs can guide initiatives related to trees in agricultural landscapes, such as biodiversity conservation and/or carbon sequestration, and in minimizing potential trade-offs with farm productivity. This will aid in decision making towards improvement of current coffee landscapes and their adaptation to climatic change. In integrating the current understanding of the coffee system, we also identify knowledge gaps related to flowering and bean maturation and hence cup quality in response to climate change with particular focus on climate extremes which require further study. The positive effect of CFE will particularly benefit intensified systems, hence significant improvements in agronomic management of smallholder systems will be required. Therefore, sustainable intensification remains an important aspect of climate change adaptation. Although we showed that shade management consists of an important adaptation strategy, increased knowledge on adequate selection and management of shade tree species will be required to maximize complementarity in the use of resources, particularly water. This will also require more insights into the impact of shade trees on nutrient complementarity and pest and disease pressure for coffee under various climate change scenarios.

## Acknowledgements

This research was funded by the Federal Ministry for Economic Cooperation and Development (BMZ),the Professorship of Ecosystem Management, ETH Zurich and the Research Program on Forest, Trees and Agriculture (FTA). It was implemented as part of the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), which is carried out with support from CGIAR Fund Donors and through bilateral funding agreements. For details please visit https://ccafs.cgiar.org/donors. The views expressed in this document cannot be taken to reflect the official opinions of these organizations. We would like to thank Bruno Rapidel and Oriana Ovalle-Rivera for sharing their insights on the CAF2014 model and Beatriz Rodriguez for helping in preparing the climate data with MarkSim. Finally, we thank two anonymous reviewers for their valuable comments.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolmodel.2018.01.009.

## References

Ainsworth, E., Long, S., 2005. What have we learned from 15 years of free-air $CO_2$ enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising $CO_2$. New Phytol. 165, 351–372.
Appelhans, T., Mwangomo, E., Otte, I., Detsch, F., Nauss, T., Hemp, A., 2016. Eco-meteorological characteristics of the sourthern slopes of Kilimanjaro, Tanzania. Int. J. Climatol. 36, 3245–3258.
Aspinwall, M., Loik, M., de Dios, V., Tjoelker, M., Payton, P., Tissue, D., 2015. Utilizing intraspecific variation in phenotypic plasticity to bolster agricultural and forest productivity under climate change. Plant Cell Environ. 38, 1752–1764.
Beer, J., Muschler, R., Kass, D., Somarriba, E., 1998. Shade management in coffee and cacao plantations. Agrofor. Syst. 38, 139–164.
Bernacchi, C., Kimball, B., Quarles, D., Long, D., Ort, D., 2007. Decreases in stomatal conductance of soybean under open-air elevation of [CO2] are closely coupled with decreases in ecosystem evapotranspiration. Plant Physiol. 134–144.
Bertrand, B., Marraccini, P., Villain, L., Breitler, J.C., Etienne, H., 2016. Healthy tropical plants to mitigate the impact of climate change – as exemplified in coffee. In: Torquebiau, E. (Ed.), Climate Change and Agriculture Worldwide. Springer, Netherlands, pp. 83–95 (chapter 7).
Beven, K., Freer, J., 2001. Equifinality, data assimilation, and uncertainty estimation in mechanistic modelling of complex environmental systems using the GLUE methodology. J. Hydrol. 249, 11–29.
Beven, K., 2008. Environmental Modelling: An Uncertain Future? Routledge, London.
Boote, K., Jones, J., Batchelor, W., Nafziger, E., Myers, O., 2003. Genetic coefficients in the CROPGRO-soybean model: links to field performance and genomics. Agron. J. 95, 32–51.
Boote, K., Jones, J., Hoogenboom, G., White, J., 2010. The role of crop systems simulation in agriculture and environment. Int. J. Agric. Environ. Inf. Syst. 1, 41–54.
Bote, A., Jan, V., 2016. Branch growth dynamics, photosynthesis, yield and bean size distribution in response to fruit load manipulation in coffee trees. Trees 30, 1275–1285.
Bote, A., Ayalew, B., Anten, N., Vos, J., 2016a. Analysis of coffee (*Coffea arabica* L.) performance in relation to radiation levels and rates of nitrogen supply I. Vegetative Growth, Production and Distribution of Biomass and Radiation Use Efficiency. PhD Thesis. Wageningen University, The Netherlands (chapter 2).
Brands, S., Herrera, S., Fernández, J., Gutiérrez, J., 2013. How well do CMIP5 earth system models simulate present climate conditions in Europe and Africa? Clim. Dyn. 41 (3–4), 803–817.
Brouwer, R., 1983. Functional equilibrium: sense or nonsense? Neth. J. Agric. Sci. 31, 335–348.
Bunn, C., Läderach, P., Ovalle Rivera, O., Kirschke, D., 2015a. A bitter cup: climate change profile of global production of Arabica and Robusta coffee. Clim. Change 129, 89–101.
Bunn, C., Läderach, P., Pérez Jimenez, J.G., Montagnon, C., Schilling, T., 2015b. Multiclass classification of agro-ecological zones for Arabica coffee: an improved understanding of the impacts of climate change. PLoS One 10 (10), e0140490. http://dx.doi.org/10.1371/journal.pone.0140490.
Cannavo, P., Sansoulet, J., Harmand, J.M., Siles Gutierrez, P., Dreyer, E., Vaast, P., 2011. Agroforestry associating coffee and *Inga densiflora* results in complementarity for water uptake and decreases deep drainage in Costa Rica. Agric. Ecosyst. Environ. 140 (1-2), 1–13. http://dx.doi.org/10.1016/j.agee.2010.11.005.
Cannell, M., 1985. Physiology of the coffee crop. In: Clifford, M., Willson, K. (Eds.), Coffee: Botany, Biochemistry and Production of Beans and Beverage. Springer, Boston, USA, pp. 108–134.
Carr, M., 2012. Chapter 5, coffee. Advances in Irrigation Agronomy. Cambridge University Press, UK, pp. 105–144.
Cavatte, P., Oliveira, A., Morais, L., Martins, S., Sanglard, L., DaMatta, F., 2012. Could shading reduce the negative impacts of drought on coffee? A morphophysiological analysis. Physiol. Plant. 144, 111–122.
Chan, K., Saltelli, A., Tarantola, S., 1997. Sensitivity analysis of model output: variance-based methods make the difference. In: Proceedings of the 1997 Winter Simulation Conference. Atlanta, Georgia.
Charbonnier, F., le Maire, G., Dreyer, E., Casanoves, F., Christina, M., Dauzat, J., Eitel, J., Vaast, P., Vierling, L., Roupsard, O., 2013. Competition for light in heterogeneous canopies: application of MAESTRA to a coffee (*Coffea arabica* L.) agroforestry system. Agric. For. Meteorol. 181, 152–169.
Charbonnier, F., Roupsard, O., le Maire, G., et al., 2017. Increased light-use efficiency sustains net primary productivity of shaded coffee plants in agroforestry system. Plant Cell Environ. http://dx.doi.org/10.1111/pce.12964.
Charles-Edwards, D., 1982. Physiological Determinants of Crop Growth. Academic Press, Sydney.
Chaves, A., Ten-Caten, A., Pinheiro, H., Ribeiro, A., DaMatta, F., 2008. Seasonal changes in photoprotective mechanisms of leaves from shaded and unshaded field-grown coffee (*Coffea arabica* L.) trees. Trees 22, 351–361.
Craparo, A., van Asten, P., Läderach, P., Jassogne, L., Grab, S., 2015. *Coffea arabica* yields decline in Tanzania due to climate change: global implications. Agric. For. Meteorol. 207, 1–10.
DaMatta, F., Ronchi, C., Maestri, M., Barros, R., 2007. Ecophysiology of coffee growth and

production. Braz. J. Plant Physiol. 19, 485–510.
DaMatta, F., Godoy, A., Menezes-Silva, P., Martins, S., Sanglard, L., Morais, L., Torre-Neto, A., Ghini, R., 2016. Sustained enhancement of photosynthesis in coffee trees grown under free-air $CO_2$ enrichment conditions: disentangling the contributions of stomatal, mesophyll, and biochemical limitations. J. Exp. Bot. 67 (1), 341–352.
Davis, A., Gole, T., Baena, S., Moat, J., 2012. The impact of climate change on indigenous Arabica coffee (*Coffea arabica*): predicting future trends and identifying priorities. PLoS One 7 (11), e47981. http://dx.doi.org/10.1371/journal.pone.0047981.
De Kauwe, M., Medlyn, B., Zaehle, S., et al., 2014. Where does the carbon go? A model-data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air $CO_2$ enrichment sites. New Phytol. 203, 883–899.
Driessen, P., 1986. The water balance of the soil. In: van Keulen, H., Wolf, J. (Eds.), Modelling of Agricultural Production: Weather, Soils and Crops. PUDOC, Wagentingen, pp. 76–116.
Duursma, R., Mäkelä, A., 2007. Summary models for light interception and light-use efficiency of non-homogeneous canopies. Tree Physiol. 27, 859–870.
Ericsson, T., Rytter, L., Vapaavuori, E., 1996. Physiology of carbon allocation in trees. Biomass Bioenergy 11, 115–127.
FAO, 2015. FAO Statistical Pocketbook: Coffee. Food and Agricultural Organization of the United Nations, Rome.
Farquhar, G., von Caemmerer, S., Berry, J., 1980. A biochemical model of photosynthetic $CO_2$ assimilation in leaves of $C_3$ species. Planta 149, 78–90.
Flexas, J., Carriqui, M., Coopman, R., Gago, J., Galmés, J., Martorell, S., Morales, F., Diaz-Espejo, A., 2014. Stomatal and mesophyll conductances to CO2 in different plant groups: underrated factors for predicting leaf photosynthesis responses to climate change? Plant Sci. 226, 41–48.
Forrester, D., 2014. A stand-level light interception model for horizontally and vertically heterogeneous canopies. Ecol. Modell. 276, 14–22.
Franck, N., Vaast, P., 2009. Limitation of coffee leaf photosynthesis by stomatal conductance and light availability under different shade levels. Trees 23, 761–769.
Fridell, G., 2014. Coffee. Polity Press, Cambridge, UK.
Fuka, D., Walter, M., Archibald, J., Steenhuis, T., Easton, Z., 2014. EcoHydRology: a community modeling foundation for Eco-Hydrology. R Package Version 0 4.12. . http://CRAN.R-project.org/package=EcoHydRology.
Gagliardi, S., Martin, A., Filho, E., Rapidel, B., Isaac, M., 2015. Intraspecific leaf economic trait variation partially explains coffee performance across agroforestry management regimes. Agric. Ecosyst. Environ. 200, 151–160.
Génard, M., Dauzat, J., Franck, N., Lescourret, F., Moitrier, N., Vaast, P., Vercambre, G., 2008. Carbon allocation in fruit trees: from theory to modelling. Trees 22, 269–282.
Ghini, R., Torre-Neto, A., Dentzien, A., Guerreiro-Filho, O., Iost, R., Patricio, F., Prado, J., Thomaziello, R., Bettiol, W., DaMatta, F., 2015. Coffee growth, pest and yield responses to free-air $CO_2$ enrichment. Clim. Change 132, 307–320.
Gifford, R., 1995. Whole plant respiration and photosynthesis of wheat under increased CO2 concentration and temperature: long-term vs. short-term distinctions for modelling. Global Change Biol. 1, 385–396.
Gifford, R., 2003. Plant respiration in productivity models: conceptualisation, representation and issues for global terrestrial carbon-cycle research. Funct. Plant Biol. 30, 171–186.
Harfoot, M., Newbold, T., Tittensor, D., Emmott, S., Hutton, J., Lyutsarev, V., Smith, M., Scharlemann, J., Purves, D., 2014. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. PLoS Biol. 12 (4), e1001841. http://dx.doi.org/10.1371/journal.pbio.1001841.
Hemp, A., 2006. The banana forests of Kilimanjaro: biodiversity and conservation of the Chagga homegardens. Biodivers. Conserv. 15, 1193–1217.
Herrera, J.C., Lambot, C., 2017. The coffee tree −genetic diversity and origin. In: Folmer, B. (Ed.), The Craft and Science of Coffee. Elsevier, pp. 1–16 (Chapter 1).
Hijmans, R., Cameron, S., Parra, J., Jones, P., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.
Hijmans, R., 2015. Raster: geographic data analysis and modeling. R Package Version 2. pp. 3–40. http://CRAN.R-project.org/package=raster.
IPCC Climate change, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boshung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA (1535 pp).
IUSS Working Group, 2015. World reference base for soil resources. World Soil Resources Reports No. 106. FAO, Rome, Italy.
Jaramillo, J., Muchugu, E., Vega, F., Davis, A., Borgemeister, C., Chabi-Olaye, A., 2011. Some like it hot: the influence and implications of climate change on coffee berry borer (*Hypothenemus hampei*) and coffee production in East Africa. PLoS One 6 (9), e24528. http://dx.doi.org/10.1371/journal.pone.0024528.
Jarvis, A., Reuter, H., Nelson, A., Guevara, E., 2008. Hole-filled SRTM for the Globe Version 4, Available from the CGIAR-CSI SRTM 90 M Database. http://srtm.csi.cgiar.org.
Jones, P., Thornton, P., 2000. MarkSim: software to generate daily weather data for Latin America and Africa. Agron. J. 92, 445–453.
Jones, C.D., Hughes, K., Bellouin, N., et al., 2011. The HadGEM2-ES implementation of CMIP5 centennial simulations. Geosci. Model. Dev. 4, 543–570.
Jonsson, M., Raphael, I., Ekbom, B., Kyamanywa, S., Karungi, J., 2015. Contrasting effects of shade level and altitude on two important coffee pests. J. Pest. Sci. 88, 281–287.
Kattge, J., Díaz, S., Lavorel, S., et al., 2011. TRY −a global database of plant traits. Global Change Biol. 17, 2905–2935.
Kropff, M.J., van Laar, H.H., 1993. Modelling Crop-weed Interactions. CAB International, Wallingford.
Lane, A., Jarvis, A., 2007. Changes in climate will modify the geography of crop suitability: agricultural biodiversity can help with adaptation. J. Semi-Arid Trop. 4 (1), 1–12.
Leenaars, J.G.B., Hengl, T., Ruiperez Gonzalez, M., Mendes de Jesus, J., Heuvelink, G.M.B., Wolf, J., van Bussel, L., Claessens, L., Yang, K.G.H., Cassman, K., 2015. Root zone plant-available water holding capacity of the sub-Saharan africa soil version 10. Gridded Functional Soil Information (dataset RZ-PAWHC SSA v. 1.0). ISRIC Report 2015/02. Collaboration Project of Africa Soil Information Service (AfSIS) and Global Yield Gap and Water Productivity Atlas (GYGA). ISRIC – World Soil Information, Wageningen, the Netherlands.
Liebig, T., Jassogne, L., Rahn, E., Läderach, P., Poehling, H.M., Kucel, P., van Asten, P., Avelino, J., 2016. Towards a collaborative research: a case study on linking science to farmers' perceptions and knowledge on Arabica coffee pests and diseases and its management. PLoS One 11 (8), e0159392. http://dx.doi.org/10.1371/journal.pone.0159392.
Long, S., Ainsworth, E., Leaky, A., Nösberger, J., Ort, D., 2006. Food for thought: lower-than-expected crop yield stimulation with rising $CO_2$ concentrations. Science 312, 1918–1921.
Luedeling, E., Kindt, R., Huth, N., Koenig, K., 2014. Agroforestry systems in a changing climate – challenges in projecting future performance. Curr. Opin. Environ. Sustain. 6, 1–7.
Luedeling, E., Smethurst, P., Baudron, F., Bayala, J., Huth, N., van Noordwijk, M., Ong, C., Mulia, R., Lusiana, B., Muthuri, C., Sinclair, F., 2016. Field-scale modeling of tree-crop interactions: challenges and development needs. Agric. Syst. 142, 51–69.
Müller, C., Cramer, W., Hare, W., Lotze-Campen, H., 2011. Climate change risks for African agriculture. PNAS 108 (11), 4313–4315.
Magrach, A., Ghazoul, J., 2015. Climate and pest-driven geographic shifts in global coffee production: implications for forest cover, biodiversity and carbon storage. PLoS One 10 (7), e0133071. http://dx.doi.org/10.1371/journal.pone.0133071.
Makowski, D., Naud, C., Jeuffroy, M., Barbottin, A., Monod, H., 2006. Global sensitivity analysis for calculating the contribution of genetic parameters to the variance of crop model prediction. Reliab. Eng. Syst. Saf. 91, 1142–1147.
Martin, A., Isaac, M., 2015. Plant functional traits in agroecosystems: a blueprint for research. J. Appl. Ecol. 52, 1425–1435.
Martins, S., Detmann, K., dos Reis, J., Pereira, L., Sanglard, L., Rogalski, M., DaMatta, 2013. Photosynthetic induction and activity of enzymes related to carbón metabolism: insights into the varying net photosyntheisis rates of coffee sun and shade leaves. Theor. Exp. Plant Physiol. 25, 62–69.
Martins, S., Galmés, J., Cavatte, P., Pereira, L., Ventrella, M., DaMatta, F., 2014a. Understanding the low photosynthetic rates of sun and shade coffee leaves: bridging the gap on the relative roles of hydraulic, diffusive and biochemical constraints to photosynthesis. PLoS One 9 (4), e9557. http://dx.doi.org/10.1371/journal.pone.0095571.
Martins, S., Araújo, W., Tohge, T., Fernie, A., DaMatta, F., 2014b. In high-light-acclimated coffee plants the metabolic machinery is adjusted to avoid oxidative stress rather than to benefit from extra light enhancement in photosynthetic yield. PLoS One 9 (4), e94862. http://dx.doi.org/10.1371/journal.pone.0094862.
Martins, L., Tomaz, M., Lidon, F., DaMatta, F., Ramalho, J., 2014c. Combined effects of elevated [$CO_2$] and high temperature on leaf mineral balance in *Coffea* spp. plants. Clim. Change 126, 365–379.
Martins, M., Rodrigues, W., Fortunato, A., Leitao, A., Rodrigues, A., Pais, I., Martins, L., Silva, M., Reboredo, F., Partelli, F., Campostrini, E., Tomaz, M., Scotti-Campos, P., Ribeiro-Barros, A., Lidon, F., DaMatta, F., Ramalho, J., 2016. Protective response mechanisms to heat stress in interaction with high [$CO_2$] conditions in *Coffea* spp. Front. Plant Sci. http://dx.doi.org/10.3389/fpls.2016.00947.
Matocha, J., Schroth, G., Hills, T., Hole, D., 2012. Integrating climate change adaptation and mitigation through agroforestry and ecosystem conservation. In: Nair, P., Garrity, D. (Eds.), Agroforestry – The Future of Global Land Use. Springer, Netherlands, pp. 105–125.
Matos, F., Wolfgramm, R., Goncalves, F., Cavatte, P., Ventrella, M., DaMatta, F., 2009. Phenotypic plasticity in response to light in the coffee tree. Environ. Exp. Bot. 67, 421–427.
Mbow, C., Smith, P., Skole, D., Duguma, L., Bustamante, M., 2014. Achieveing mitigation and adaptation to climate change through sustainable agroforestry practices in Africa. Curr. Opin. Environ. Sustain. 6, 8–14.
Monsi, M., Saeki, T., 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jpn. J. Bot. 14, 22–52.
Montagnon, C., Marraccini, P., Bertrand, B., 2012. Breeding for coffee quality. In: Oberthür, T., Läderach, P., Pohlan, H., Cook, J. (Eds.), Specialty Coffee: Managing Quality. International Plant Nutrition Institute, Southeast Asia Program.
Monteith, J., 1977. Climate and the efficiency of crop production in Britain. Philos. Trans. R. Soc. Lond. 281, 277–294.
Morton, J., 2007. The impact of climate change on smallholder and subsistence agriculture. Proc. Natl. Acad. Sci. U. S. A. 104, 19680–19685.
Nicotra, A., Atkin, O., Bonser, S., Davidson, A., Finnegan, E., Mathesius, U., Poot, P., Purugganan, M., Richards, C., Valaladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15 (12), 684–692.
Niinemets, Ü., Flexas, J., Peñuelas, J., 2011. Evergreens favored by higher responsiveness to increased $CO_2$. Trends Ecol. Evol. 26 (3), 136–142.
Ordonez, J., Luedeling, E., Kindt, R., Lestara Tata, H., Harja, D., Jamnadass, R., van Noordwijk, M., 2014. Constraints and opportunities for tree diversity management along the forest transition curve to achieve multifunctional agriculture. Curr. Opin. Environ. Sustain. 6, 54–60.
Otte, I., Detsch, F., Mwangomo, E., Hemp, A., Appelhans, T., Nauss, T., 2016. Multidecadal trends and interannual variability of rainfall as observed from five lowland stations at Mt. Kilimanjaro, Tanzania. J. Hydrometeorol. 18 (2), 349–361.
Ovalle-Rivera, O., Läderach, P., Bunn, C., Obersteiner, M., Schroth, G., 2015. Projected shifts in *Coffea arabica* suitability among major global producing regions due to

climate change. PLoS One 10 (4), e0124155. http://dx.doi.org/10.1371/journal.pone.0124155.
Ovalle-Rivera, O., 2014. Impacto del cambio climático en al productividad de café (Coffea arabica) bajo sistemas agroforestales en Costa Rica y Nicaragua. Master thesis. Centro Agronómico Tropical de Investigación y Enseñenza (CATIE), Turrialba, Costa Rica (URL:). http://repositorio.bibliotecaorton.catie.ac.cr/bitstream/handle/11554/7204/Impacto_del_cambio_climatico.pdf;jsessionid=426080B22C242F2CB326613530DD199C?sequence=1.
Padovan, M., Cortez, V., Navarrete, L., Navarrete, E., Deffner, A., Centeno, L., Munguía, R., Barrios, M., Vílchez-Mendoza, J., Vega-Jarquín, C., Costa, A., Brook, R., Rapidel, B., 2015. Root distribution and water use in coffee shaded with Tabebuia rosea Bertol. And Simarouba glauca DC compared to full sun coffee in sub-optimal environmental conditions. Agrofor. Syst. 89, 857–868.
Penman, H.L., 1948. Natural evaporation for open water, bare soil and grass. Proc. R. Soc. Lond. Ser. A 193, 120–146.
Perez, J., Menendez, M., Menendez, F., Losada, I., 2014. Evaluating the performance of CMIP3 and CMIP5 global climate models over the north-east Atlantic región. Clim. Dyn. 43 (9–10), 2663–2680.
Poorter, H., Nagel, O., 2000. The role of biomass allocation in the growth response of plants to different levels of light, $CO_2$, nutrients and water: a quantitative review. Aust. J. Plant Physiol. 27, 595–607.
Poorter, H., Lambers, H., Evans, J., 2014. Trait correlation networks: a whole-plant perspective on the recently criticized leaf economic spectrum. New Phytol. 201 (2), 378–382.
Pujol, G., Iooss, B., Janon, A., et al., 2015. Sensitivity: sensitivity analysis. R Package Version 1.11.1. . http://CRAN.R-project.org/package=sensitivity.
Core Team, R., 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL: http://www.R-project.org/.
Ramirez-Villegas, J., Jarvis, A., 2010. Disaggregation of Global Circulation Model Outputs. International Center for Tropical Agriculture (CIAT), Cali, Colombia.
Ramirez-Villegas, J., Challinor, A., Thornton, P., Jarvis, A., 2013. Implications of regional improvement in global climate models for agricultural impact research. Environ. Res. Lett. 8 (2), 024018.
Reyer, C., Leuzinger, S., Rammig, A., et al., 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Glob. Change Biol. 19, 75–89.
Reyer, C., Flechsig, M., Lasch-Born, P., van Oijen, M., 2016. Integrating parameter uncertainty of a process-based model in assessments of climate change effects on forest productivity. Clim. Change 137 (3), 395–409.
Rice, R., 2011. Fruits from shade trees in coffee: how important are they? Agrofor. Syst. 83, 41–49.
Rodrigues, W., Machado, J., da Silva, J., de Assis, F., Ferraz, L., da Silva, L., de Abreu, D., de Paula, W., Cespom, L., de Sousa, E., Glenn, D., Ramalho, J., Campostrini, E., 2016. Whole-canopy gas exchanges in *Coffea* sp. is affected by supra-optimal temperature and light distribution within the canopy: the insights from an improved multi-chamber system. Sci. Hortic. 211, 194–202.
Rodriguez, D., Cure, J., Cotes, J., Gutierrez, A., Cantor, F., 2011. A coffee agroecosystem model: I. Growth and development of the coffee plant. Ecol. Modell. 222 (3626–2639).
Saltelli, A., Bolado, R., 1998. An alternative way to compute Fourier amplitude sensitivity test (FAST). Comput. Stat. Data Anal. 26 (4), 445–460.
Saltelli, A., Tarantola, S., Chan, K., 1999. A quantitative model-independent method for global senstivity analysis of model output. Technometrics 41 (1), 39–56.
Sanchez, P., 1995. Science in agroforestry. Agrofor. Syst. 30, 5–55.
Schaller, M., Schroth, G., Beer, J., Jiménez, F., 2003. Species and site characteristics that permit the association of fast-growing trees with crops: the case of *Eucalyptus deglupta* as coffee shade in Costa Rica. For. Ecol. Manage. 175, 205–215.
Schroth, G., Läderach, P., Dempewolf, J., Philpott, S., Haggar, J., Eakin, H., Castillejos, T., Garcia, J., Soto, L., Hernandez, R., Eitzinger, A., Ramirez-Villegas, J., 2009. Towards a climate change adaptation strategy for coffee communities and ecosystems in the Sierra Madre de Chiapas, Mexico. Mitig. Adapt. Strat. Glob. Change 14, 605–625.
Siles, P., Vaast, P., Dreyer, E., Harmand, J.M., 2010. Rainfall partitioning into throughfall, stemflow and interception loss in a coffee (*Coffea arabica* L.) monoculture compared to an agroforestry system with *Inga densiflora*. J. Hydrol. 395, 39–48.
Sinclair, T., Seligman, N., 1996. Crop modeling: from infancy to maturity. Agron. J. 88 (5), 698–704.
Sobol', I.M., 1993. Sensitivity estimates for nonlinear mathematical models. Math. Model. Comput. Exp. 14, 407–414.
Staver, C., Guharay, G., Monterroso, D., Muschler, G., 2001. Designing pest-suppressive multistrata perennial crop systems: shade-grown coffee in Central America. Agrofor. Syst. 53, 151–170.
Tausend, P., Meinzer, F., Goldstein, G., 2000. Control of transpiration in three coffee cultivars: the role of hydraulic and crown architecture. Trees 14, 181–190.
Thornton, P., Ericksen, P., Herrero, M., Challinor, A., 2014. Climate variability and vulnerability to climate change: a review. Glob. Change Biol. 20, 3313–3328.
Unigarro, C., Jaramillo, A., Ibarra, L., Flórez, C., 2016. Canopy structure and theoretical coefficient of extinction in genotypes of arabic coffee in Colombia. Acta Agron. 65, 383–389.
Vaast, P., Bertrand, B., Perriot, J.J., Guyot, B., Génard, M., 2005. Fruit thinning and shade improve bean characteristics and beverage quality of coffee (Coffea arabica L.) under optimal conditions. J. Sci. Food Agric. 86 (2), 197–204.
Vaast, P., van Kanten, R., Siles, P., Angrand, J., Aguilar, A., 2008. Biophysical interactions between timber trees and Arabica coffee in suboptimal conditions of Central America. In: Jose, S., Gordon, A. (Eds.), Toward Agroforestry Design. Springer, Netherlands, pp. 133–146.
Vaast, P., Martínez, M., Boulay, A., Castillo, B., Harmand, J.M., 2015. Diversifying Central American coffee agroforestry systems via revenue of shade trees. In: Ruf, F., Schroth, G. (Eds.), Economics and Ecology of Diversification. Springer, Netherlands, pp. 271–281.
Vaast, P., Harmand, J.-M., Rapidel, B., Jagoret, P., Deheuvels, O., 2016. Coffee and cocoa production in agroforestry – a climate-smart agriculture model. In: Torquebiau, E. (Ed.), Climate Change and Agriculture Worldwide. Springer, Netherlands, pp. 209–224 (Chapter 16).
Van Ittersum, M., Cassman, K., Grassini, P., Wolf, J., Tittonell, P., Hochman, Z., 2013. Yield gap analysis with local to global relevance – a review. Field Crops Res. 143, 4–17.
Van Kanten, R., Vaast, P., 2006. Transpiration of arabica coffee and associated shade tree species in sub-optimal, low altitude conditions of Costa Rica. Agrofor. Syst. 67, 187–202.
Van Keulen, H., 1986. A simple model of water-limited production. In: Van Keulen, H., Wolf, H. (Eds.), Modelling of Agricultural Production: Weather, Soils and Crops. Simulation Monogr., PUDOC, Wageningen, pp. 130–152.
Van Oijen, M., Leffelaar, P., 2008. Lintul-2: wáter Limited Crop Growth. Wageningen University Plant Sciences(URL: http://models.pps.wur.nl/node/944. Accessed 16 February 2016).
Van Oijen, M., Dreccer, M., Firsching, K., Schnieders, B., 2004. Simple equations for dynamic models of the effects of $CO_2$ and $O_3$ on light-use efficiency and growth of crops. Ecol. Modell. 179, 39–60.
Van Oijen, M., Rougier, J., Smith, R., 2005. Bayesian calibration of process-based forest models: bridging the gap between models and data. Tree Physiol. 25, 915–927.
Van Oijen, M., Dauzat, J., Harmand, J.-M., Lawson, G., Vaast, P., 2010a. Coffee agroforestry systems in Central America: I. A review of quantitative information on physiological and ecological processes. Agrofor. Syst. 80, 341–359.
Van Oijen, M., Dauzat, J., Harmand, J.-M., Lawson, G., Vaast, P., 2010b. Coffee agroforestry systems in Central America: II. Development of a simple process-based model and preliminary results. Agrofor. Syst. 80, 361–378.
Van Oijen, M., Schapendonk, A., Höglind, M., 2010c. On the relative magnitudes of photosynthesis, respiration, growth and carbon storage in vegetation. Ann. Bot. 105, 793–797.
Van Vuuren, D., Edmonds, J., Kainuma, M., et al., 2011. The representative concentration pathways: an overview. Clim. Change 109, 5–31.
Van der Vossen, H., 2005. A critical analysis of the agronomic and economic sustainability of organic coffee production. Exp. Agric. 41 (4), 449–473.
Van der Wolf, J., Jassogne, L., Gram, G., Vaast, P., 2016. Turning local knowledge on agroforestry into an online decision-support tool for the tree selection in smallholders' farms. Exp. Agric. 1–17. http://dx.doi.org/10.1017/S001447971600017X.
Wang, E., Smith, C., Bond, W., Verburg, K., 2004. Estimation of vapour pressure deficit and crop water demand in APSIM and their implications for prediction of crop yield, water use, and deep drainage. Aust. J. Agric. Res. 55, 1227–1240.
Wang, N., Jassogne, L., van Asten, P., Mukasa, D., Wanyama, I., Kagezi, G., Giller, K., 2015. Evaluating coffee yield gaps and important biotic, abiotic, and management factors limiting coffee production in Uganda. Eur. J. Agron. 63, 1–11.
Wintgens, 2004. The coffee plant. In: Wintgens, J. (Ed.), Coffee: Growing, Processing, Sustainable Production. Wiley-VCH Verlag, Germany.
Yin, X., Struik, P., Kropff, M., 2004. Role of crop physiology in predicting gene-to-phenotype relationships. Trends Plant Sci. 9 (9), 426–432.
Yin, X., 2013. Improving ecophysiological simulation models to predict the impact of elevated atmospheric $CO_2$ concentration on crop productivity. Ann. Bot. 112, 465–475.
Zhang, Z., Cai, Z., Liu, G., Wang, H., Huang, L., Cai, C., 2017. Effects of fertilization on the growth, photosynthesis, and biomass accumulation in juvenile plants of three coffee (*Coffea arabica* L.) cultivars. Photosynthetica 55 (1), 134–143.
Zuidema, P., Leffelaar, P., Gerritsma, W., Mommer, L., Anten, N., 2005. A physiological production model for cocoa (*Theobroma cacao*): model presentation, validation and application. Agric. Syst. 84, 195–225.